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Reassignment of Some *Caryospora* Species (Apicomplexa: Eimeriidae) to *Eumonospora* (Apicomplexa: Sarcocystidae) and a Summary of Caryosporid-like Coccidians of Vertebrates

Donald W. Duszynski

Department of Biology, University of New Mexico, Albuquerque, NM, 87131, USA

Abstract

This review was crafted to clear up some of the current confusion regarding the correct taxonomic placement of those apicomplexan coccidians that produce unique monosporocystic octosporozoic (1 sporocyst with 8 sporozoites) oocysts during the sexual phase of their life history in vertebrate hosts. Currently, such oocysts have been placed in 1 of 4 genera, *Avispora*, *Caryospora*, *Karyospora*, or *Eumonospora,* 2 of which are no longer accepted or useful (*Avispora* and *Karyospora*). My review suggests that to present (2023) there are 62 valid *Caryospora* and 26 valid *Eumonospora* species. *Caryospora* species are recorded from a bird (1), lizards (4), snakes (56), and a turtle (1), and *Eumonospora* species are recorded from birds (25) and a mammal (1). In addition to the morphotypes with (more-or-less) valid binomials in both genera, there are an additional 24 *Caryospora*-like forms mentioned in the literature that do not yet have sufficient structural or genetic information to have merited a binomial and, therefore, must be designated as *species inquirendae*; these include 5 in birds, 2 in lizards, 1 in a mammal, and 16 in snakes. Similarly, 4 *Eumonospora* morphotypes in birds and 1 in a mammal also must be designated *species inquirendae*. Vertebrate hosts reported to have been infected with 1 or more species of these 2 genera include: **birds:** 14 families, 23 genera, 40 species; **lizards:** 3 families, 3 genera, 4 species; **mammals:** 2 families, 2 genera, 2 species; **snakes:** 10 families, 54 genera, 83 species; and **turtles:** 1 family, 1 genus, 1 species. Finally, such infections occur worldwide and have been documented in vertebrates in 43 countries on 6 of 7 continents on Earth (except Antarctica).

Avispora, *Caryospora*, *Karyospora*, or *Eumonospora*? That is the question. Léger (1904) published a note of 2 short paragraphs about protozoan parasites found in the intestine of the European asp, *Vipera apis* (L., 1758). In the first paragraph, he named a new species of *Trichomastix*; his second paragraph named "two new coccidia a *Diplospora*, *D. fragilis* n. sp. and another very special Coccidia characterized by its oocysts containing a single octospore sporocyst" and said, "this Coccidia which becomes the type of a new family, the name of *Karyospora simplex*, n. sp." Technically, the name became a *species inquirenda* since it was not accompanied by any mensural data or a picture or line drawing. Seven years later, however, Léger (1911) published a more complete description that included measurements and line drawings of endogenous stages and a sporulated oocyst, but he changed the spelling of the genus name to *Caryospora*, never once mentioning the name *Karyospora* or why he changed the spelling. Addressing that issue, Reichenow (1919) dated Léger's creation of the genus name to 1911. However, Pellérdy (1974, p. 126) explained, "According to Article 23(b) of the International Commission of Zoological Nomenclature London, 1961, the senior synonym *Karyospora* should now be regarded as a *nomen oblatum*, since the spelling *Caryospora* has been adopted for more than 50 years."

Allen (1933) also described a coccidium with octosporozoic and monosporocystic oocysts from the intestine of the eastern turkey buzzard, *Cathartes aura septentrionalis* Wied-Neuwied, 1839; at the time, she suggested it belonged to a new genus and species in the Eimeriidae, subfamily Caryosporinae, and named her new form *Eumonospora tremula*. Her new genus differed from *Caryospora* by having oocysts without a micropyle (M) and sporocysts with a distinct residuum (SR) but lacking a Stieda (SB) and substieda body (SSB). Hoare (1934), a prominent force in parasitology at the time, felt strongly that Allen's terminology, "only introduced undesirable complication and confusion into the classification of the coccidia" (p. 7). Bowing to the pressure, Allen (1934) emended her name to *Caryospora tremula* (Allen, 1933) Hoare, 1934.

Since then, many new species of *Caryospora* have been described from birds, snakes, lizards, 1 turtle, and even a mammal (1 named species), but no changes in the taxonomy or classification of the genus were proposed until Schuster et al. (2016) suggested transferring all avian *Caryospora* species into a new genus, *Avispora*. A few authors (e.g., Cardozo et al., 2017, 2019) followed suit, but most did not. However, molecular sequencing and phylogenetic analysis at 2 loci, 18S rRNA and COI, have begun to demonstrate that there are genetic distinctions between caryosporan-like isolates (Carreno and Barta, 1999; Barta et al., 2001; Yang et al., 2014; Liu et al., 2020) and that some species are more closely related to sarcocystids (sporocysts without SB) than to eimeriids (sporocysts with SB and SSB). Furthering this work, Chou et al. (2020, 2021) resurrected the genus *Eumonospora* Allen, 1933 as a member of the Sarcocystidae Poche, 1913 to include all caryosporan species without SBs and made replacement names to *Eumonospora* for 25 former *Caryospora* species (Chou et al., 2020). However, they made some omissions in their work, and the oocyst details of each species they transferred to *Eumonospora* were not given. Thus, there is still work to be done to completely summarize the current status of these 2 groups of Coccidia. Here I attempt to complete this process.

Results

Note: All measurements are in micrometers (μm).

Caryospora *and* Eumonospora *species known from vertebrates*

Characterization of Caryospora *Léger, 1904*

Wacha and Christiansen (1982) provided the most useful definition of this genus, which I have adapted here for its utility. Heteroxenous with primary and secondary hosts in which gamogony occurs in each. In the primary host, development occurs in the intestinal epithelium, resulting in the formation of unsporulated oocysts. In the secondary host, endogenous development is extraintestinal, resulting in the formation of monosporocystic oocysts with 1 sporocyst and 8 sporozoites (SZ) and caryocysts each with 1 SZ, both of which are infective. Sporogony is exogenous in the primary host and endogenous in the secondary host. Primary hosts are mainly birds and reptiles, while secondary hosts are mammals only, to date.

Caryospora *species in birds (1)*

***Caryospora jiroveci* Cerná, 1976**

Type host: Erithacus rubecula (L., 1758), European robin (Muscicapidae)

Other hosts: None to date.

Type locality: Czech Republic: Prague.

Sporulated oocyst: Spheroidal; number of walls: 1, ~1 thick; wall characteristics: thin, transparent; L × W (N = 40): 19–22 wide; L/W ratio: 1.0; M, oocyst residuum (OR), both absent; polar granule (PG), 1–2 present.

Sporocyst and sporozoites: Ovoidal; L × W (N = 40): 17–19 × 13–14; L/W ratio: ~1.3; SB, SSB: both present; SR: present; SR characteristics: loose, scattered granules in the center of sporocyst between SZ (line drawing); SZ: not described but pictured in cross-section as circles (line drawing).

Prevalence: From 1972 to 1973, Cerná (1976) collected 306 fecal samples from various free-living birds (mostly Passeriformes) in the vicinity of Prague; 1/9 (11%) European robins collected had oocysts of this caryosporan in its feces.

Sporulation: Exogenous. Černá (1976) said that sporulation required more than 4 days in 1.5% potassium dichromate ($K_2Cr_2O_7$) solution at room temperature.

Remarks: This is the only caryosporan described from birds and, unfortunately, it has not been reported again since its discovery by Černá (1976). Initially, I thought it best to list it as a *species inquirenda*. However, Dr. Černá (1976) provided both a photomicrograph of a sporocyst, which clearly has an SB-SSB complex, and a quality line drawing, so I believe it is more prudent to give her the benefit of the doubt. Certainly, the validity of this caryosporan in robins and other Passeriformes in Europe, and elsewhere, should continue to be studied.

Caryospora *species in lizards (4)*

***Caryospora ernsti* Upton, Current and Barnard, 1984b**

Type host: Anolis carolinensis Voigt, 1832, North American green anole (Anolidae).

Other hosts: None to date.

Type locality: Unknown. All lizards were housed at the Atlanta Zoo, Georgia, USA; their records showed the lizards originated from a private supply outlet in La Place, Louisiana, USA. *Anolis carolinensis* is found throughout the southeastern USA and extends south into Bolivia and Paraguay.

Sporulated oocyst: Spheroidal; number of walls: 1, ~1.0 thick; wall characteristics: lightly pitted, colorless; L × W (N = 50): 12.5 (11–14.5); L/W ratio: 1.0; M, OR: both absent; PG: varies in shape from spheroidal to ovoidal to irregular, 1.3 (1.0–1.5) wide, highly refractile, attached to inner surface of oocyst wall; sometimes 1–2 other nonrefractile granules are attached to the inner surface of the oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W (N = 50): 10.7 × 8.3 (10–12.5 × 7.5–9); L/W ratio: 1.3 (1.2–1.4); SB, SSB: present; SB: 2.2 wide × 0.7 high (2–3 × 0.5–1); SSB: 3.2 wide × 1.1 high (2.5–4 × 1–1.5); SR: numerous granules, each 0.3–1.5 wide, condensed into a single mass, L × W: 5.6 × 3.8 (4–6 × 3–5), in center of sporocysts between SZs (line drawing); SZ: sausage-shaped (line drawing), L × W (N = 50): 9.7 × 2.0 (8–11 × 2), with 1 end slightly pointed; refractile bodies (RB): spheroidal to ovoidal, about 1–3 wide, 1 anterior and 1 posterior, with a round nucleus (N) between them.

Prevalence: Upton et al. (1984b) reported this species in 4/11 (36%) of the captive *A. carolinensis* they examined from the Atlanta Zoo.

Sporulation: Exogenous. Oocysts kept in 2.5% aqueous (w/v) potassium dichromate solution ($K_2Cr_2O_7$) sporulated within 24 hours at 25–28°C.

Remarks: Upton et al. (1984b) said they saw meronts, gametes, and unsporulated oocysts in the epithelium of the anterior one-half of the small intestine.

Caryospora gekkonis Chakravarty and Kar, 1947

Type host: Gecko gecko (L., 1758), Tokay gecko (Gekkonidae).

Other hosts: None to date.

Type locality: India: suburbs of Kolbata (= Calcutta).

Description of sporulated oocyst: Spheroidal; number of walls: 2; wall characteristics: outer, is drawn out at 1 place to form a M (?); L × W: 20; L/W ratio: 1.0; M: present; OR, PG: both absent.

Description of sporocyst and sporozoites: Subspheroidal; L × W: 11; L/W ratio: 1.0; SB: present as a distinct knob-like structure at pointed end of sporocyst; SSB, parastieda body (PSB): both absent; SR: present; SR characteristics: composed of granules that fill the sporocyst and surround the SZ; SZ: conspicuous structures that appear spheroidal when viewed on end.

Prevalence: Found in the only specimen of the type host examined by Chakravarty and Kar (1947).

Sporulation: Exogenous. Oocysts were kept in 2.5% aqueous (w/v) potassium dichromate solution ($K_2Cr_2O_7$), but only a few of them sporulated within 48 hours.

Remarks: According to Chakravarty and Kar (1947), this was the first species of *Caryospora* found and described both from India and from a lizard. Their description of the SZ should be looked at cautiously because they stated, "arrangement of the SZ in the sporocyst could not be observed as further growth of the oocysts was checked" (whatever that means). This description is marginal by even the most lenient standards.

Caryospora natchitochesensis McAllister, Seville and Connior, 2014

Type host: Anolis carolinensis Voigt, 1832, North American green anole (Anolidae).

Other hosts: None to date.

Type locality: USA: Louisiana: Natchitoches Parish, 8.5 km SE of Natchitoches (31°41′48.4″N, 93°03′10.8″W).

Sporulated oocyst: Subspheroidal to ovoidal; number of walls: 2, ~0.3–0.7 thick; wall characteristics: outer, smooth, yellow-brown pigmented; L × W (N = 22): 13.1 × 12.3 (11–15 × 10–14); L/W ratio: 1.1 (1.0–1.2); M, OR: both absent; PG: 1, attached to inner surface of oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W (N = 22): 10.1 × 7.4 (7–13 × 6–10); L/W ratio: 1.4 (1.1–1.5); SB: present; SSB: absent; SR: granules or globules are dispersed among SZs; SZ: sausage-shaped, with both anterior and posterior RBs present as spheroidal to ovoidal bodies, with a round N between them.

Prevalence: McAllister et al. (2014) found this species in 1/18 (6%) *A. carolinensis* they examined and the only one from Natchitoches Parish.

Sporulation: Endogenous and exogenous. Oocysts were passed partially and fully sporulated.

Remarks: McAllister et al. (2014) said the sporulated oocysts of this "species" closely resembled those of *C. ernsti*, described 3 decades earlier, also from *A. carolinensis*, but that they differed by (1) being slightly subspheroidal and having a bilayered wall (vs. 1 layer), and its wall contained yellow-brown pigment, while that of *C. ernsti* was colorless; and (2) having sporocysts in this form that have an SSB that was found lacking in the original description of *C. ernsti*. In my opinion, these trivial differences are not sufficient to have named a new caryosporan species from the same host species that is common throughout the southeastern USA, especially since it was found in only 1 host animal collected from the same state (Louisiana) in the USA.

***Caryospora varaniornati* Modrý, Šlapeta, Knotek and Koudela, 2001**

Type host: Varanus (*Polydaedalus*) *ornatus* (Daudin, 1803), ornate monitor (Varanidae).

Other hosts: None to date.

Type locality: Benin (1 of 16 West African countries).

Sporulated oocyst: Spheroidal to slightly subspheroidal; number of walls: 1, ~0.75 thick; wall characteristics: smooth colorless; L × W: 12.0 × 11.5 (11–12.5 × 11–12); L/W ratio: 1.0 (1.0–1.1); M, OR: both absent; PG: 1, small, ~1.0–1.5.

Sporocyst and sporozoites: Broadly ellipsoidal; L × W: 8.8 × 6.7 (8.5–9.5 × 6.5–7); L/W ratio: 1.3 (1.2–1.5); SB: present, lentil-like, ~0.5 high × 1.0 wide; SSB: may be present but was not visible to Modrý et al. (2001); SR: present; SR characteristics: small granules scattered among SZ; SZ: elongate, each with subspheroidal RB and a centrally located N.

Prevalence: Modrý et al. (2001) found it in 2/2 (100%) ornate monitors (in the Zoo Brno) that had been imported from Africa into the Czech Republic. Both monitors shared a single cage.

Sporulation: Exogenous. Modrý et al. (2001) stated that oocysts were unsporulated when collected from the monitors. Fecal samples from both monitors were stored in 2.5% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution at ~4°C for 1 month before they were studied, but Modrý et al. (2001) said they saw fully sporulated oocysts at day 13 after collection.

Remarks: The authors (2001) said they were not able to definitively document an SSB, but 1 photomicrograph (their Fig. 3, p. 8) showed a distinct space under the small SB that may represent an SSB. Modrý et al. (2001) inoculated 10^3 sporulated oocysts of this species *per os* into 2 juvenile 6-month-old Nile monitors, *Varanus niloticus* (L., 1766) from Togo (West Africa) that had been housed separately from the ornate monitors and were coprologically negative for at least 2 months prior to infection. One of the 2 Nile monitors was given dexamethasone 2 days prior to inoculation. Feces were monitored for oocysts for 3 months but were always negative. Modrý et al. (2001) also orally inoculated 3 severe combined immunodeficient (SCID) mice, which were maintained in isolation, with 10^3 sporulated oocysts. The Nile monitor treated with dexamethasone and the SCID mice were killed 30 days post-infection (DPI) (mice) and 90 DPI (monitor), and 26 tissues were fixed, embedded in paraffin, and processed for light microscopy. No developmental stages of a coccidian were found, and the SCID mice did not develop typical dermal caryosporosis. To the casual reader, the title of this paper by Modrý et al. (2001) might be confusing because it states that *C. varaniornati* is described from the "Nile monitor, *V. niloticus* species complex," while the abstract says it was described from the ornate Nile monitor, *V. ornatus*. Only 2 other *Caryospora* species are described from saurians: *C. gekkonis*, from *Gekko gocko* (Gekkonidae) in India (Chakravarty and Kar, 1947), and *C. ernsti*, from *Anolis carolinensis* (Anolidae), which were housed in the Atlanta Zoo (Upton et al., 1984b). This species is distinguished from *C. gekkonis*, which has much larger oocysts and an M. The sporulated oocysts of this species somewhat resemble those of *C. ernsti* but have slightly larger oocysts and sporocysts, and its sporocysts have a distinct and easily seen SSB, while those of this species do not. Also, the hosts of all 3 caryosporans are phylogenetically distinct and geographically distant from each other.

Caryospora *species in snakes (56)*

***Caryospora ahaetullae* Modrý and Koudela, 1994**

Type host: Ahaetulla nasuta (Lacépède, 1789), long-nosed vine snake (Colubridae).

Other hosts: Ahaetulla prasina (Boie, 1827), Gunther's or oriental whipsnake (Colubridae).

Type locality: Thailand: Larn Sang (near Tag).

Sporulated oocyst: Spheroidal-subspheroidal; number of walls: 1, ~0.75 thick; wall characteristics: yellow, smooth; L × W (N = 50): 24.8 (22.5–26); L/W ratio: 1.1; M, OR: both absent; PG: 1–2 RB present, 1.5–2 wide, variable in shape, usually attached to inner surface of oocyst wall.

Sporocyst and sporozoites: Ellipsoidal; L × W (N = 50): 18.5 × 14.2 (18–19.5 × 13–15); L/W ratio: 1.3; SB, SSB, SR: all present; SB: 3.2 × 3.0 (3–4 × 2.5–3.5); SSB; 4.2 × 1.2 (4–4.5 × 1–1.5); SR: numerous small, scattered granules; SZ: vermiform, 15.0 × 3.8 (13.5–16.5 × 3.5–4.5), each with prominent transverse striations and 2 spheroidal RBs.

Prevalence: Found in 2/2 (100%) specimens of the type host; later, Modrý and Koudela (1998) found this species a second time in 1/4 (25%) *A. nasuta* collected in India in a snake also infected with *C. veselyi*.

Sporulation: Exogenous. Oocysts became fully sporulated within 3 days at 20–25°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: Line drawing and 2 photomicrographs included to support their description. This species most closely resembles *C. duszynskii* Upton et al. (1984a) and *C. madagascariensis* Upton, Freed, et al. (1990). See the comparisons made by Modrý (1998, p. 32) and Modrý and Koudela (1994, p. 234).

***Caryospora barnardae* Upton, Freed, Burdick and McAllister, 1990**

Type host: Liopholidophis stumpffi (Boettger, 1881), Malagasy colubrid (Colubridae).

Other hosts: None to date.

Type locality: Madagascar.

Sporulated oocyst: Spheroidal; number of walls: 2, 0.8–1.0 thick; wall characteristics: outer lightly pitted, inner is smooth, of equal thickness; L × W (N = 25): 13.7 (11–15); L/W ratio: 1.0; M, OR: both absent; PG: 1 present, 1.6 wide, usually associated with inner surface of oocyst wall.

Sporocyst and sporozoites: Ellipsoidal to ovoidal; L × W (N = 25): 11.1 × 8.8 (10–14 × 8–10); L/W ratio: 1.3 (1.2–1.4); SB, SSB, SR: all present; SB: flat, 0.6–0.8 × 2.0–2.4; SSB: faint, same size as SB; SR: 10–20 globules, each 0.2–2.0 wide, scattered in sporocyst; SZ: vermiform, 10.4 × 2.6 (9–12 × 2–3), each with 2 RB, a central one, 3.2 × 2.4 (2–4 × 2–3) and a posterior RB, 1.9 × 1.8 (1–3 × 1–2).

Prevalence: Found in the only specimen of the type host examined.

Sporulation: Unknown, oocysts sporulated in the field before they reached the lab to be examined.

Remarks: Line drawing and 2 photomicrographs included with the description. This species is most similar to *C. bigenetica* from North American crotalids, to *C. ernsti* from an anole, and to *C. jararacae* from *Bothrops* in South America. Upton, Freed, et al. (1990) provided some modest reasons for separating their form from these 3 species.

***Caryospora bengalensis* Mandel, 1976**

Type host: Enhydris enhydris Schneider, 1799, rainbow or striped water snake (Colubridae).

Other hosts: None to date.

Type locality: India: West Bengal, Chakdah Nadia District.

Sporulated oocyst: Spheroidal; number of walls: 2; wall characteristics: smooth, very thin; L × W (N = 50): 21.5 (20–22.5); L/W ratio: 1.1; M, OR: both absent; PG: present, attached to the inner surface of the oocyst wall.

Sporocyst and sporozoites: pear–shaped; L × W (N = 50): 19.0 × 13.5 (18–20.5 × 12–14); L/W ratio: 1.4; SB, SSB, SR: all present; SB: a "shiny plug"; SSB; faint, not visible in line drawing; SR: many variable-sized refractile granules, scattered within sporocyst; SZ: bean-shaped, 10–12 × 2.5; RB, N: absent or not mentioned.

Prevalence: Found in ~30/50 (60%) specimens of the type host examined.

Sporulation: Exogenous. Oocysts sporulated in 24–38 hours at 30–32°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: One small (22 mm) line drawing was included. Mandal (1976) examined 50 *E. enhydris* and said 30 were infected with 2 species of coccidia that included this caryosporan and *Eimeria fibrilosa*; he then explained that most were infected with both species except in a few in which monospecific infections were encountered. His drawing showed a micropyle, as did Léger's (1911), but Upton, Current, et al. (1983) have shown this structure in *C. simplex* is a PG attached to the inner surface of the oocyst wall.

***Caryospora bigenetica* Wacha and Christiansen, 1982**

Type host: Crotalus horridus L. 1758, timber or cane-brake rattlesnake (Viperidae).

Other hosts: Agkistrodon contortrix L., 1766, copperhead; *Crotalus adamanteus* Palisot de Beauvois, 1799, eastern diamondback rattlesnake; *Crotalus atrox* Baird and Giraud, 1853, western diamondback rattlesnake; *Sistrurus catenaus* (Rafinesque, 1818), massasauga (natural and experimental infections); *Sistrurus miliaris* L., 1766, pigmy rattlesnake (all Viperidae).

Type locality: USA: Iowa, Madison County.

Sporulated oocyst: Spheroidal; number of walls: 2, ~1.0 thick; wall characteristics: smooth, outer mamillated, ~2/3 of total thickness and appears striated in optical cross-section; L × W (N = 50): 13.2 (11–15); L/W ratio: 1.0; M, OR: both absent; PG: present, attached to the inner surface of the oocyst wall.

Sporocyst and sporozoites: ellipsoidal, ovoidal, or pyriform; L × W (N = 50): 10.1 × 7.7 (8–11.5 × 6.5–9); L/W ratio: 1.3; SB, SSB, SR: all present; SB: discoidal of uniform thickness, 1.6 × 0.9 (1–2 × 0.75–1); SSB: same width as SB; SR: a cluster of several spheroidal bodies, each ~1–2 wide; SZ: lanceolate, 8.0 × 2.0; RB: 2, 1 anterior and 1 posterior in SZ.

Prevalence: Wacha and Christiansen (1982) found this species in at least 3 *C. horridus* from Madison County and in 1 *S. catenatus* from Mills County, Iowa. Upton et al. (1986) reported that *A. contortrix* and *S. catenatus*, both from Georgia, also represented natural hosts but did not give any numbers of snakes collected or snakes infected.

Sporulation: Exogenous. Oocysts sporulated in 5–6 days at 22–25°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: Nine line drawings and 21 photomicrographs were presented of both endogenous and exogenous developmental stages of this species by Wacha and Christiansen (1982) who did experimental infections of mice with *C. bigenetica* oocysts from a forest rattlesnake (*Crotalus* sp.). On day 4 post-inoculation (DPI) the mouse was fed to a coccidia-free dwarf rattlesnake (*Sistrus* sp.), and the snake began to discharge unsporulated oocysts on 9 DPI. Four mice that were infected with oocysts either died or were killed on 8, 10, 12, and 32 DPI and various endogenous stages (micro-, macrogamonts, sporocysts, caryocysts) of *C. bigenetica* were found in connective tissues of the tongue, skin, and subcutaneous tissue.

Thus, they completed Koch's postulates by demonstrating that mice infected with oocysts from snakes were later infective for snakes in which both asexual (merogony) and sexual (gamogony) stages occurred in their intestine, resulting in the discharge of unsporulated oocysts into the environment. Oocysts of *C. bigenetica* are very similar to oocysts of *C. simplex*, but *C. bigenetica* appears to be more pathogenic to mice than is *C. simplex* (Upton et al., 1986).

One of the remarkable characteristics of the life cycle of *C. bigenetica* is the ability of its sporulated oocysts to infect certain mammals and develop extensively in them. For example, Upton and Barnard (1988) infected laboratory mice *per os* with sporulated oocysts collected from the feces of either the northern copperhead, *A. contortrix*, or the eastern diamondback rattlesnake, *C. adamanteus*, and found numerous developmental stages in the connective tissues of the cheek, nose, tongue, and scrotum. These stages included: Type I meronts and merozoites at 8 DPI; Type II meronts and merozoites at 10 DPI; Type III meronts and merozoites at 10 DPI; both micro- and macrogametocytes at 10–12 DPI; unsporulated oocysts at 10–14 DPI; sporulated oocysts at 12–14 DPI; and SZ in caryocysts at 12–14 DPI (Upton and Barnard, 1988, Table 1, p. 16). Developmental stages of *C. bigenetica* were also recorded in fibroblast-like cells of the connective tissue of the cheek, nose, scrotum, and tongue of all inoculated mice from 8–60 DPI, and 4 mice infected intraperitoneally with 4×10^5 free SZ had similar developmental stages of *C. bigenetica* in the connective tissues of their cheek, nose, and tongue at 8 and 10 DPI.

Sundermann, Lindsay, et al. (1988) described *in vitro* development of *C. bigenetica* using SZ excysted from oocysts collected from a captive timber rattlesnake, *C. horridus*; these SZ were inoculated onto cultures of cotton rat primary testicle cells, cotton rat kidney cells, and human fetal lung cells. The development of *in vitro* stages they documented included intracellular SZs at 1 DPI, first-generation meronts at 2 DPI, first-generation merozoites at 3 DPI, second-generation meronts and merozoites at 5 DPI, microgametocytes and macrogamonts at 9 DPI, unsporulated oocysts at 10 DPI, sporulated oocysts and extracellular SZs at 11 DPI, and SZ in caryocysts at 16 DPI (Sundermann, Lindsay, et al., 1988, Table 1, p. 468). Thus, *C. bigenetica* can complete its entire life cycle *in vitro* in cells of host or nonhost origin. Although *C. bigenetica* and *C. simplex* are similar in some aspects of their life history, Sundermann, Lindsay, et al. (1988) discussed the subtle timing, size, and pathogenic effects that distinguish one from the other.

Douglas et al. (1991) demonstrated that 7 different routes of inoculation could produce viable infections, and pathology, in Swiss-Webster mice and that the site of development of *C. bigenetica* in host tissues was independent of experimental inoculation route. They used clean suspensions of oocysts (3.3×10^4) and sporocysts (5.7×10^4) to inoculate 3 mice each by mouth, intraperitoneal, intravenous, intramuscular, subcutaneous, dermal, and intraocular injections. All mice showed clinical signs of dermal coccidiosis at 9 DPI, regardless of inoculation route. Developmental stages of *C. bigenetica* were found in the muzzle, tongue, footpad, lumbar subcutaneous tissue, biceps femoris muscle, conjunctiva, and eye, and pathological signs included swelling of the facial tissue, footpads, and scrota (male mice).

A number of authors have used *C. bigenetica* oocysts and sporocysts to infect a variety of mammalian hosts and cell cultures experimentally to determine the timing and developmental stages in various cell types and locations; this includes the work done by Douglas and Sundermann (1992); Douglas et al. (1988, 1991); Douglas, Sundermann, and Lindsay (1992); Douglas, Sundermann, Lindsay and Mulvaney (1992); Lindsay, Sundermann and Blagburn (1988); and Sundermann et al. (1989). Koudela (1993) also collected *C. bigenetica* oocysts from a western diamondback rattlesnake, *C. atrox*, housed in a zoo in the Czech Republic to infect common voles, *Microtus arvalis* Pallas, 1778; gerbils, *Meriones unguiculatus* (Milne-Edwards, 1867); and pigs, *Sus scrofa domesticus* L., 1758. All experimentally infected animals displayed clinical signs of dermal coccidiosis, including swelling of the face, ears, footpads, and scrota or vagina. Gerbils developed more severe clinical signs of infection and had a higher mortality rate than voles. Transmission of *C. bigenetica* caryocysts between voles and mice, between mice and voles, voles and gerbils, and voles and pigs were demonstrated. Koudela (1993) thus demonstrated that *C. bigenetica* can be transmitted by predation or cannibalism between different species of rodents and pigs. Finally, Sundermann (unpublished data in Lindsay and Sundermann, 1989) found that an isolate of *C. bigenetica* was infectious for mice and cotton rats but not for Norway rats, marmosets, and domestic chickens.

***Caryospora bothriechis* Seville, Asmundsson and Campbell, 2005**

Type host: Bothriechis aurifer Salvin, 1860, yellow-blotched palm pit viper (Viperidae).

Other hosts: None.

Type locality: Guatemala: Baja Verapaz, Cerro Verde, near La Unión Barrios, 15°22.37′N, 89°48.91′W.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, ~0.8 thick; wall characteristics: smooth, outer ~2/3 of total thickness; L × W (N = 15): 12.7 × 12.5 (12–14 × 12–13); L/W ratio: 1.0; M, OR: both absent; PG: 1, highly refractile, adjacent to inner surface of the oocyst wall.

Sporocyst and sporozoites: ovoidal; L × W: 9.0 × 7.5 (8–10 × 7–8); L/W ratio: 1.2; SB: present, faint, clear; SSB: absent; SR: present, a few disbursed small granules; SZ: sausage-shaped, not measured; RB: not observed.

Prevalence: Seville et al. (2005) discovered this species in 1/3 (33%) specimens of the type host.

Sporulation: Unknown. Oocysts sporulated in the field.

Remarks: One line drawing and 3 photomicrographs were presented to support this species description. This is the first *Caryospora* reported from *Bothriechis*. This species is somewhat similar to *C. simplex* but is much smaller and has other structural differences (Seville et al., 2005).

***Caryospora brygooi* Upton, Freed, Burdick and McAllister, 1990**

Type host: Madagascarophis colubrinus (Schlegel, 1837), Madagascar cat-eye snake (Pseudoxyrhophiidae).

Other hosts: None to date.

Type locality: Madagascar.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, ~0.8–1.0 thick; wall characteristics: outer, moderately pitted, ~3/4 of total thickness, and inner layer, 0.4, smooth; L × W (N = 25): 20.2 × 19.7 (19–22 × 18–21); L/W ratio: 1.0; M, OR: both absent; PG: 1, adjacent to inner surface of the oocyst wall.

Sporocyst and sporozoites: ellipsoidal; L × W (N = 25): 16.2 × 12.0 (14–18 × 11–13); L/W ratio: 1.35 (1.3–1.4); SB: present, 1.3 high × 2.8 wide (1–2 × 2–3); SSB: present, 1.9 high × 3.8 wide (1–3 × 3–4); SR: present, numerous small granules scattered among SZ; SZ: elongate, banana-shaped, 14.8 × 3.1 (14–16 × 3), each with anterior transverse striations and containing 2–3 RBs.

Prevalence: Upton, Freed, et al. (1990) discovered this species in the feces of 1/4 (25%) specimens of the type host.

Sporulation: Unknown. Oocysts sporulated in the field.

Remarks: Upton, Freed, et al. (1990) discussed the 9 other ophidian *Caryospora* species known from snakes at that time and gave their view on how this species differed from those described earlier.

***Caryospora brasiliensis* Carini, 1932**

Type host: Philodryas aestivus (Duméril, Bibron and Duméril, 1854) (syn. *Dryophylax aestivus* Duméril, Bibron and Duméril, 1854), Brazilian or common green racer (Colubridae).

Other hosts: Erythrolamprus poecilogyrus (Wied-Neuwied, 1824), cobra verde; *Leimadophis poecilogyrus schotti* (Schlegel, 1837), cobra-corredeira (Carini, 1939); *Philodryas nattereri* (Steindachner, 1870), Paraguay green racer (Carini, 1939); *Philodryas olfersii* (Lichtenstein, 1823), Lichtenstein's green racer (Carini, 1939; Lainson and Shaw, 1973) (all Colubridae).

Type locality: Brazil: São Paulo State.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 3, ~1–2 thick; wall characteristics: outer, smooth, thin, colorless; middle, ~2/3rds of total thickness, prominently striated; inner layer, smooth; L × W (N = 50): 21.7 × 20.8 (19–24 × 18–24); L/W ratio: 1.0; M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal, with 1 end drawn out into a neck; L × W (N = 50): 16.1 × 12.2 (16–19 × 12–18); L/W ratio: 1.3; SB: caplike; SSB: present (in line drawing), wider than SB; SR: a compact mass of many granules scattered among and surrounding SZ; SZ: elongate, banana-shaped, 14.8 × 3.1 (14–16 × 3), with anterior transverse striations, each containing 2–3 RBs.

Prevalence: Found in the only specimen of the type host examined by Carini (1932, 1933) and in 1/1 of each of the other host species reported to harbor this parasite.

Sporulation: Exogenous. Oocysts discharged unsporulated (Lainson and Shaw, 1973), but the sporulation time is still unknown.

Remarks: Carini published identical species descriptions and naming of this form twice (1932, 1933), in 2 different journals (see Literature Cited). He also published the type host name as *Chlorosoma aestivum*, a binomial that does not currently exist in the Reptile Database (Uetz et al., 2023), but which Lainson and Shaw (1973) say was a synonym of *P. aestivus*. Carini's original description(s) (1932, 1933) were marginal at best, but he did include a useful line drawing that showed the presence of an SSB not mentioned in his description. Lainson and Shaw (1973) redescribed this species in more detail, and their metrics are used in the oocyst and sporocysts dimension above. They (1973) also included 2 useful line drawings of sporulated oocysts, but these did not include the SSB seen in Carini's drawing. Lainson and Shaw (1973) also reported that meronts and gametes were located in the epithelium of the small intestine. Carini (1939) later reported seeing oocysts of *C. brasiliensis* in *L. p. schotti*, *P. nattereri*, and *P. olfersii*.

***Caryospora carajasensis* Lainson, Nascimento and Shaw, 1991**

Type host: Oxyrhopus petola digitalis (Reuss, 1834), forest flame snake (Colubridae).

Other hosts: None to date.

Type locality: Brazil: Pará State, Serra dos Carajás (6°S, 50°18'W).

Sporulated oocyst: Spheroidal (13%) to subspheroidal (73%); number of walls: 2, ~1.2 thick; wall characteristics: outer, thicker, with a rough surface bearing coarse

striations (pores?); inner, smooth; L × W (N = 50): 22.9 × 21.5 (20–25 × 19–24); L/W ratio: 1.1 (1.0–1.2); M, OR, PG: all absent.

Sporocyst and sporozoites: Broadly ellipsoidal; L × W (N = 50): 17.5 × 12.9 (16–19 × 11–14); L/W ratio: 1.3 (1.3–1.5); SB, SSB, SR: all present; SB: nipple- or stopper-like; SSB: conspicuous, about same width as SB (line drawing); SR: a central compact mass of granules or globules surrounded by the SZs like the staves of a barrel or irregularly scattered with the SZs in sporocyst; 1 or 2 RBs in each SZ.

Prevalence: Unknown.

Sporulation: Unknown.

Remarks: Lainson et al. (1991) looked at the feces of "a number of snakes from Amazonia Brazil" when they described this species, but they failed to record the number of snakes infected with *C. carajasensis*.

***Caryospora ceadsensis* Tobias de Santana Miglionico and Viana, 2017**

Type host: Siphlophis pulcher (Raddi, 1820), Guanabara spotted night snake (Dipsadidae).

Other hosts: None to date.

Type locality: Brazil: Rio de Janeiro State, Angra dos Reis municipality, Ilha Grande (23°11′07.6″S, 44°11′25.9″W).

Sporulated oocyst: Spheroidal to slightly subspheroidal; number of walls: 2, ~1.3 thick; wall characteristics: inner layer, smooth, outer slightly striated; L × W (N = 56): 22.1 × 22.0 (17–24 × 17–24); L/W ratio: 1.0 (1.0–1.1); M, OR: both absent; PG: 1, highly refractive body near inner surface of the oocyst wall (line drawing).

Sporocyst and sporozoites: Ellipsoidal; L × W (N = 56): 14.7 × 11.2 (11–17 × 10–13); L/W ratio: 1.3 (1.0–1.5); SB: nipple-like, dark, and dense, 1.1 high × 2.9 wide; SSB: bubble-shaped, 1.7 high × 3.8 wide (1–2 × 3–4.5); SR: numerous small granules disbursed among SZ; SZ: elongate, banana-shaped, 14.8 × 3.1 (14–16 × 3); SZ with striations, but no other details were given.

Prevalence: Tobias de Santana Miglionico and Viana (2017) recovered oocysts of this species in the feces of the only specimen of the type host examined.

Sporulation: Unknown. Oocysts sporulated in the field.

Remarks: Tobias de Santana Miglionico and Viana (2017) reported (Table 1, p. 624) that 5 other named caryosporans were known from dipsadid snakes in Brazil prior to their discovery; these included *C. brasiliensis*, *C. carajasensis*, *C. olfersii*, *C. paraensis*, and *C. pseustesi* (Carini, 1932, 1933, 1939; Lainson and Shaw, 1973; Lainson et al., 1991), and another, *C. zacapensis*, from a colubrid in Guatamala (Seville et al., 2005) that had similar oocysts. Using presence/absence of a PG, SSB, striations on SZs, composition of the SR, size of the various sporocysts, and size and structure of SSBs, they said they could distinguish this species from the others relatively easily.

***Caryospora choctawensis* McAllister, Roehrs and Seville, 2013**

Type host: Tantilla gracilis Baird and Girard, 1853, flathead snake (Colubridae).

Other hosts: None to date.

Type locality: USA: Oklahoma, Choctaw County, Fort Towson Historic Site, Post Cemetery off US 70, County Road E2060 (34.025801°N, 95.258803°W).

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2; wall characteristics: thick, smooth; L × W (N = 10): 15.8 × 15.0 (14–18 × 14–16); L/W ratio: 1.1 (1.0–1.2); M, OR: both absent; PG: 1, bilobed, closely associated with inner surface of the oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W (N = 10): 10.8 × 9.0 (10–12 × 8–9); L/W ratio: 1.2 (1.0–1.5); SB: present, nipple-like (line drawing), not measured; SSB: present, described as "bubble-like," not measured; SR: present, many granules in a compact mass; SZ: elongate, banana-shaped, with some anterior transverse striations, each containing 2 RBs.

Prevalence: McAllister et al. (2012) discovered this species in the feces of 1/15 (7%) specimens of the type host that included 1/2 (50%) in Choctaw County, OK, 0/6 from Arkansas, and 0/7 from Texas.

Sporulation: Exogenous. Oocysts were passed unsporulated or partially sporulated, and some completed sporulation in 5 days at 23°C, while others never sporulated.

Remarks: One line drawing and 3 photomicrographs were presented to support the original description. McAllister et al. (2012) compared the sporulated oocysts of this form to those of *C. gracilis* described from *T. gracilis* in Texas and Arkansas, USA (Upton, McAllister, et al., 1992), to *C. relictae* and *C. tantillae* from *T. relicta* in Florida, USA (Telford, 1997), and to *C. durelli* from the Round Island boa, *Casarea dussumieri*, in Mauritius (Daszak et al., 2011a) but found the oocyst and sporocyst sizes and the presence/absence of certain structures (OR) to clearly separate these 5 caryosporans from each other.

***Caryospora cobrae* Nandi, 1985**

Type host: Naja naja (L., 1758), common or spectacled cobra (Elapidae).

Other hosts: None to date.

Type locality: India: West Bengal, Burdwan.

Sporulated oocyst: Spheroidal to slightly subspheroidal; number of walls: 2, ~0.75 thick; wall characteristics: smooth, outer wall is relatively thin and inner wall is somewhat thicker; L × W (N = 30): 18.5 × 17.2 (16.5–19.5 ×

16.5–18); L/W ratio: 1.1 (1.0–1.1); M: reported as present by Nandi, but there was no photomicrograph, and her line drawing looks like a PG attached to the outside wall of the oocysts; OR, PG: both absent.

Sporocyst and sporozoites: Piriform; L × W (N = 15): 14.2 × 11.8 (12–16.5 × 9–13); L/W ratio: 1.2; SB: distinct, nipple-like (line drawing), not measured; SSB: absent; SR: "beaded, intermingled with SZs"; SZ: sausage-shaped, narrowly ovoidal, L × W (N = 15): 5.4 × 2.0 (5–6.5 × 1–3); N of SZ centrally placed, but no RBs were visible.

Prevalence: Found in the only specimen of the type host examined by Nandi (1985).

Sporulation: Nandi (1985) said sporulation was complete at 48–72 hours at room temperature.

Remarks: The description of this "species" is incomplete and inadequate by current-day standards. As noted, I believe it likely that there is no M on the oocyst and that what Nandi (1985) believed to be an M was actually a PG attached to the inner wall of the oocyst, as we have seen in so many caryosporan oocysts described from snakes. It is also important to note that this form has not been found since its initial description by Nandi (1985).

***Caryospora colubris* Matuschka, 1984b**

Type host: Hierophis (syn. *Coluber*) *viridiflavus* (Lacépède, 1798), green or western whip snake (Colubridae).

Other hosts: Dolichophis jugularis (L., 1758) (syn. *Coluber jugularis* L., 1758), large whip snake; *Hemorrhois hippocrepis* (L., 1758) (syn. *Coluber hippocrepis* L., 1758), horseshoe whip snake; *Eirenis decemlineatus* (Duméril, Bibron et Duméril, 1854), [no English common name]; (all Colubridae).

Type locality: Italy: Sicily.

Sporulated oocyst: Spheroidal to slightly subspheroidal; number of walls: 2, ~1.0 thick; wall characteristics: thick, smooth; L × W (N = 100): 16.2–27.9 wide; L/W ratio: 1.0; Matuschka (1984a) divided oocysts into 3 categories: 90% of the oocysts were L × W (N = 50): 25.7 (23.5–27.9), 10% were L × W (N = 25): 20.8 (20.6–22.1), and ~1% were L × W (N = 25): 17.4 (16.2–18.2); M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal (line drawing); L × W (N = 100): 13.2–19.1 × 10.3–14.7; L/W ratio: means not given; sporocysts corresponding to the 3 oocyst size groups (above) were, L × W: 17.9 × 12.7 (17.6–19 × 12–15), L × W: 15.0 × 12.0 (15–16 × 12), and L × W: 14.5 × 11.0 (13–15 × 10–12); SB: discoidal of uniform thickness; SSB: hemispheroidal, slightly less wide than SB (line drawing); SR: a cluster of several spheroidal bodies; SZ: sausage-shaped (line drawing), but no details given.

Prevalence: Matuschka (1984b) recovered oocysts of this species in 3/3 (100%) specimens of the type hosts (*H.* [= *C.*] *viridiflavus*) he examined from Sicily. Paperna and Finkelman (1991) reported this species in 2/2 (100%) naturally infected Syrian black snakes (*D. jugularis*) collected in Israel, and Modrý (1998) reported finding oocysts representing this species in 1/3 (33%) *H. hippocrepis*, in 1/2 (50%) *H.* (= *C.*) *viridiflavus*, and in 2/7 (29%) *E. decemlineatus* in the Czech Repubic.

Sporulation: Exogenous. Most oocysts sporulated in 48–72 hours at 23°C, after they were placed in 1–2.5% (w/v) aqueous potassium dichromate solution ($K_2Cr_2O_7$).

Remarks: Matuschka (1984b) divided the sporulated oocysts he found into 3 categories based on oocyst and sporocyst sizes; despite these differences he assumed that the oocysts represented the same species. Earlier, Bray (1960) reported similar results—3 size categories of caryosporan oocysts from *Psammophis sibilans phillipsi*—but he assigned a separate specific epithet for each category. Clearly, someone must sequence a few genes from each of these 6 size categories to determine who was right.

Paperna (1991) described the ultrastructure (TEM) of endogenous developmental stages (merogony, microgamonts, macrogamonts, oocysts) of *C. colubris* in 1 *D. jugularis* experimentally infected with sporulated oocysts. Paperna and Finkelman (1991) studied the endogenous development of *C. colubris* in intestinal epithelial cells of 2 naturally infected Syrian black snakes collected near Rehovot, Israel; they reported that feces from these infected snakes discharged oocysts for a period of 11 months, and in 1 experimentally infected snake, oocysts appeared in the feces up to 7 months post-infection (PI). They (1991) also inoculated sporulated oocysts *per os* into 10 white mice, killed 2 months PI, and into 2 rough-tailed rock agamas, *Laudakio* (syn. *Agama*) *stellio* (L., 1758), killed 1 and 3 months PI, but found no tissue stages. Their lab-infected snake began discharging unsporulated oocysts 18 DPI, and they said that an M was present, but an OR and a PG were not. They (1991) briefly described, measured, and provided photomicrographs (their Figs. 1K–M) and line drawings (their Figs. 2–15) for several developmental stages (SB/SSB complex, meronts, merozoites, micro- and macrogamonts, young oocysts), but they never again mentioned or provided evidence for the presence of an M.

Modrý (1998) qualified his identifying *C. colubris* oocysts from *E. decemlineatus*: "…. prevalence of this species in insectivorous *E. decemlineatus* seems unlikely. *Caryospora colubris* is a species with wide range of morphometrical data, which fully overlap measurements of isolates from Jordan. Without transmissional studies or other (e.g., molecular) data [it] is impossible to exclude the conspecificity of both species. Therefore, this isolate is considered as *Caryospora* cf. *colubris*. The exact status of this coccidium found in Jordanian *E. decemlineatus* requires further research" (p. 30).

Upton et al. (1984a) and Matuschka (1986b) said that *C. colubris* oocysts from snake feces were not infectious for mice, suggesting that not all species of *Caryospora* have life cycles that use 2 hosts. It is also possible that this species may use a different taxonomic group of vector hosts besides mice.

***Caryospora coniophanis* Seville, Asmundsson and Campbell, 2005**

Type host: Coniophanes imperialis (Kennicott in Baird, 1859), black-striped snake (Colubridae).

Other hosts: None.

Type locality: Guatemala: Petén, in front of Biotopo Cerro Cahui (16°58.82′N, 89°42.30′W).

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, 1.3 thick; wall characteristics: outer yellow-brown, pitted, ~2/3 of total thickness; L × W (N = 10): 18.8 × 18.1 (17–20.5 × 16–20); L/W ratio: 1.0; M, OR: both absent; PG: 1, large, refractile, adjacent to inner surface of the oocyst wall.

Sporocyst and sporozoites: ovoidal; L × W: 13.2 × 9.4 (12–15 × 8–10); L/W ratio: 1.4; SB, SSB: both present; SR: present, a central mass of compact granules with a few disbursed small granules; SZ: sausage-shaped, curled around central SR; RB, N: not observed.

Prevalence: Seville et al. (2005) discovered this species in the only specimens of the type host they examined.

Sporulation: Unknown. Oocysts sporulated in the field.

Remarks: One line drawing and 3 photomicrographs were presented to support this description. This was the first *Caryospora* species described from *Coniophanes*. These oocysts are most similar to those of *C. tantillae* and *C. relictae*, both described from *Tantillae relicta* in Florida; however, they are smaller than those of *C. tantillae*, and although similar in size to those of *C. relictae*, the presence of a pitted outer wall and smaller sporocysts distinguishes them from each other (Seville et al., 2005).

***Caryospora conophae* Seville, Asmundsson and Campbell, 2005**

Type host: Conophis imperialis (Duméril, Bibron and Duméril, 1854), road guarder snake (Colubridae).

Other hosts: None.

Type locality: Guatemala: Zacapa, San Vicente, Area El Arenal (14°10.05′N, 90°58.01′W).

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, ~1.4 thick; wall characteristics: outer, yellow-brown, pitted, ~2/3 of total thickness; L × W (N = 20): 20.4 × 19.5 (17–26 × 17–25); L/W ratio: 1.0; M, OR: both absent; PG: 1, large, refractile, adjacent to inner surface of the oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W: 13.1 × 9.8 (11–15 × 8–11); L/W ratio: 1.3; SB: nipple-like; SSB: a large globular body; SR: a central compact mass of granules with a few disbursed small granules; SZ: sausage-shaped, 8–10 × 2–3, curled around central SR; RB, N: not observed.

Prevalence: Seville et al. (2005) discovered this species in 3/4 (75%) specimens of the type host they examined.

Sporulation: Unknown. Oocysts sporulated in the field.

Remarks: One line drawing and 3 photomicrographs were presented to support their description of a new species. This was the first *Caryospora* reported from *Conophis*. Sporulated oocysts of this form are most similar to those of *C. tantillae* but have larger oocysts with a thicker wall and have a distinct, prominent PG attached to the inner oocyst wall.

***Caryospora constanciae* Lainson, Nascimento and Shaw, 1991**

Type host: Micrurus spixii spixii Schmidt and Walker, 1943, Amazonian coral snake (Elapidae).

Other hosts: None to date.

Type locality: Brazil: Rondônia, area of the hydroelectric dam "Samuel" (8°45′S, 63°28′W).

Sporulated oocyst: Spheroidal (12%) to predominantly subspheroidal (88%); number of walls: 2, ~1.9–2.5 thick; wall characteristics: outer has an irregular surface that often is lost in handling; inner, 1.2 thick, is smooth; L × W (N = 50): 22.9 × 21.5 (20–25 × 19–24); L/W ratio: 1.1 (1.0–1.2); M, OR, PG: all absent.

Sporocyst and sporozoites: Broadly ellipsoidal; L × W (N = 50): 17.5 × 12.9 (16–19 × 11–14); L/W ratio: 1.3 (1.3–1.5); SB, SSB, SR: all present; SB: nipple- or stopper-like; SSB: conspicuous, about same width as SB (line drawing); SR: a central compact mass of granules or globules surrounded by the SZs like the staves of a barrel or irregularly scattered with the SZs in sporocyst; 1 or 2 RBs in each SZ.

Prevalence: Unknown.

Sporulation: Unknown.

Remarks: Lainson et al. (1991) looked at the feces of "a number of snakes from Amazonia Brazil" when they described this species, but they failed to record the number of snakes infected with *C. carajasensis*.

***Caryospora corallae* Matuschka, 1984b**

Type host: Corallus cainus (L., 1758), Emerald tree boa (Boidae).

Other hosts: None to date.

Type locality: French Guayana, an overseas Department of France, North Coast of South America.

Sporulated oocyst: Spheroidal; number of walls: 2, ~1.0 thick; wall characteristics: colorless, smooth; L × W:

18.7–24.6 (22.4); L/W ratio: 1.0; M, OR: both absent; PG: present, attached to inner surface of oocyst wall (his Fig. 2, p. 359).

Sporocyst and sporozoites: Elongate ovoidal; L × W: 19.1 × 13.1 (18–20 × 12–14); L/W ratio: 1.5; SB, SR: both present; SSB: reported as absent; SB: at tapered end of sporocyst; SR: a cluster of several spheroidal bodies, surrounded by the SZ; SZ: arranged around the SR, completely filling the sporocyst.

Prevalence: Oocysts were reported in 3/3 (100%) specimens of the type host.

Sporulation: Exogenous. Oocysts sporulated in 5–6 days at 23°C in 2.2% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: Naming this as a new *Caryospora* species was based mainly on the structural dimensions of its sporulated oocysts when compared to those of *C. brasiliensis*, *C. bigenetica*, *C. jaracae*, and *C. lampropeltis* (Matuschka, 1984a, Table 1, p. 359), in addition to both host and geographic differences. Upton et al. (1984a) and Matuschka (1986b) said that *C. corallae* oocysts from snake feces were not infectious for mice, suggesting that not all species of *Caryospora* have life cycles that use 2 hosts.

***Caryospora demansiae* Cannon, 1967**

Type host: Demansia psammophis (Schlegel, 1857), yellow-faced whip snake (Elapidae).

Other hosts: None to date.

Type locality: Australia: Queensland, near Brisbane.

Sporulated oocyst: Subspheroidal; number of walls: 2, only ~0.6 thick; wall characteristics: colorless, smooth, but small, dark tubercles of undetermined nature sometimes covered oocysts freshly recovered from gut contents, but were rarely present in oocysts isolated from the feces; L × W: 20.4 × 19.8 (16–27 × 14–27); L/W ratio: 1.0+; M, OR: both absent; PG: 1 or more sometimes present.

Sporocyst and sporozoites: Elongate ovoidal; L × W: 13.1 × 10.8 (11–16 × 8–13); L/W ratio: 1.2; SB, SSB, SR: all present; SB: at tapered end of sporocyst, 1.0 high × 2.0 wide; SSB: a clear, "refringent" globule that becomes less visible as oocyst ages; SR: a compact mass of granules surrounded by the SZs; SZ: banana-shaped (line drawing), slightly longer than sporocyst with 1 RB in each SZ (not shown in line drawing).

Prevalence: Cannon (1967) found this species in 4/6 (67%) specimens of the type host he examined.

Sporulation: Cannon (1967) argued that most oocysts sporulated in the intestinal lumen of the gut in infected snakes; knowing this raised 2 issues in his thinking: (1) coupled with the irregularity of defecation in snakes, he felt that studies on sporulation time and prepatent period were of no diagnostic value, and (2) it would be interesting to determine if oocysts that have sporulated in the gut lumen could release their SZ and produce autoinfection.

Remarks: Cannon (1967) fixed, embedded, and sectioned infected intestinal tissue in which he reported the following endogenous stages, supranuclear, in intestinal epithelial cells: (1) numerous trophozoites, ~4 wide; (2) meronts, 6–12 wide with 4, 8, or 16 sausage-shaped merozoites, each about 3 × 1.5–5, and each with an anterior globule; (3) mature macrogametocytes, 10–18 wide, with peripherally arranged wall-forming bodies; (4) thin-walled, saclike microgametocytes, ~12 wide, each with a few microgametes; and (5) zygotes with a chromophilic periphery. Cannon (1967) noted that the oocysts he found and described were somewhat similar to those of 5 other caryosporans known from snakes: *C. brasiliensis*, *C. hermae*, *C. weyerae*, *C. zuckermannae*, and *C. japonium*, but he explained the differences between them all to satisfy his decision to name his oocysts as a new species.

***Caryospora dendrelaphis* Cannon and Rzepczyk, 1974**

Type host: Dendrelaphis punctulatus (Gray 1826), common tree snake (Colubridae).

Other hosts: None to date.

Type locality: Australia; Queensland, Brisbane.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, ~1.0 thick; wall characteristics: smooth; L × W (N = 36): 21.4 × 20.7 (12–25.5 × 12–24); L/W ratio: 1.0; M, OR, PG: all absent.

Sporocyst and sporozoites: Elongate ovoidal; L × W (N = 33): 14.8 × 11.7 (10–18 × 8.5–14); L/W ratio: 1.3; SB, SSB, SR: all present; SB: nipple-like (line drawing), 2 high × 2 wide; SSB: present, but indistinct; SR: a central compact mass of granules completely filling the sporocyst; SZ: slightly longer than the sporocyst and spiraled around the SR.

Prevalence: Cannon and Rzepczyk (1974) found *C. dendrelaphis* in 2/5 (40%) specimens of the type host they examined.

Sporulation: Exogenous. Oocysts took 24–48 hours at 25–28.5°C to fully sporulate.

Remarks: Cannon and Rzepczyk (1974) noted that unsporulated oocysts were slightly smaller than sporulated oocysts; L × W (N = 39): 20.2 × 19.6 (15–24 × 14–24). They also fixed, embedded and sectioned infected intestinal tissue in which they found: (1) small trophozoites, 3–6 wide; (2) meronts, 5–9 wide with 16, 32, or 64 stumpy merozoites, each about 1.5 × 1; (3) thin-walled microgametocytes 10–14 wide with numerous club-shaped microgametes; (4) mature macrogametocytes, 11–20 × 9–15, with foamy cytoplasm and wall-forming bodies; and (5) a few zygotes, each with a weakly staining oocyst wall. Macrogametes

were the most numerous stage seen, and most developmental stages were above the N, proximal to the lumen in the duodenum.

***Caryospora durrelli* Daszak, Ball, Streicker, Jones and Snow, 2011a, b**

Type host: Casarea dussumieri (Schlegel, 1837), Round Island boa (Bolyeridae).

Other hosts: None.

Type locality: Mauritius: Round Island, on the west slope, 21 km NNE of Mauritius (19°50′16″S, 57°46′34″E).

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, ~1.0 thick; wall characteristics: outer, smooth, ~0.6 thick, inner, 0.4 thick; L × W (N = 20): 19.2 × 18.2 (17.5–21 × 16–21); L/W ratio: 1.05 (1.0–1.1); M, OR, PG: all absent.

Sporocyst and sporozoites: Ellipsoidal; L × W (N = 20): 14.7 × 11.0 (13–16 × 9.5–11.5); L/W ratio: 1.3; SB: nipple-like, 0.4 high × 1.6 wide; SSB: 1.2 wide × 2.0 high; SR: compact, composed of numerous granules, 12 × 4.5, surrounded by SZs; SZ and their RBs were not clearly seen (Daszak et al., 2011a, b).

Prevalence: Daszak et al. (2011a) discovered this species in 6/11 (55%) specimens of the type host they examined; these included in 6/10 snakes (including one immature specimen) in 1993 and 0/1 snake collected in 1995.

Sporulation: Unknown. Oocysts sporulated in the field.

Remarks: One line drawing and 3 photomicrographs were presented to support their new description. The Bolyeridae contains only 1 extant species, *C. dussumieri*, which is endemic to Mauritius; the only other species in this family, *Bolyeria multocarinata*, is presumably extinct (Daszak et al., 2011a). This is the only coccidian described to date from this species/family, and because of its geographic isolation it is likely a valid species. Daszak et al. (2011a) also compared the oocysts of this species to those of *C. corallae* from the emerald tree boa, *Corallus caninus*, in French Guiana (Matuschka, 1984) and those of *C. epicratesi* from the rainbow boa, *Epicrates cenchria*, in Brazil (Lainson et al., 1991), but the differences between the 3 types of oocysts and sporocysts were distinct. Daszak et al. (2011b) published an erratum correcting the misspelling of the parasite's name from *C. durelli* to *C. durrelli*.

***Caryospora duszynskii* Upton, Current and Barnard, 1984a**

Type host: Pantherophis guttatus (L., 1766) (syn. *Coluber guttata* L., 1766), red or eastern corn snake (Colubridae).

Other hosts: Pantherophis emoryi (Baird et Girard, 1853), Great Plains rat snake (Colubridae) (McAllister, 1989; McAllister et al., 1995; McAllister et al., 2011); *Pantherophis obsoletus* (Say, 1823) (syn. *Coluber obsoletus* Say, 1823), black rat snake (Colubridae) (Upton et al., 1984a; McAllister, 1989; McAllister et al., 1995; McAllister et al., 2011); *Lampropeltis calligaster* (Harlan, 1827), prairie kingsnake (Colubridae) (McAllister et al., 2011); *Lampropeltis holbrooki* (Stejneger, 1902), speckled king snake (Colubridae) (McAllister et al., 2011); *Lampropeltis triangulum* (Lacépède, 1789), eastern milksnake (Colubridae) (McAllister et al., 2011); *Masticophis flagellum* (Shaw, 1802), coachwhip (Colubridae) (Upton et al., 1994; McAllister, 2011).

Type locality: USA: Georgia.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, ~1.5 thick; wall characteristics: outer is heavily pitted to give a coarse, striated appearance and is ~2/3 of total thickness, inner layer, 0.5, smooth; L × W (N = 50): 25.7 × 24.3 (23–28.5 × 22–28); L/W ratio: 1.1 (1.0–1.1); M, OR: both absent; PG: 1, rarely 2, variable in shape, L × W (N = 50): 1.8 × 1.6 (1.5–3.5 × 1.5–2.0) attached to inner surface of the oocyst wall, often along with some "debris."

Sporocyst and sporozoites: Ovoidal; L × W (N = 50): 18.3 × 14.8 (17–21.5 × 13.5–16.5); L/W ratio: 1.2 (1.1–1.3); SB: prominent, 1.6 high × 3.8 wide (1.5–2.0 × 3.5–4.5); SSB: present, 2.1 high × 4.5 wide (1.5–3.5 × 3.5–5.5); SR: present, L × W (N = 50): 11.4 × 6.3 (9–13.5 × 5.5–7.5), numerous spheroidal granules, 1.0–2.5 wide, around which SZs are arranged; SZ: elongate banana-shaped (line drawing), 15.8 × 3.6 (13–19.5 × 3–4.5); SZ with anterior and posterior RBs and a spheroidal N between them.

Prevalence: Upton et al. (1984a) discovered unsporulated oocysts of this species in the feces of 1 *P. guttatus* that was suffering from anorexia in the Atlanta Zoo. Later, they examined the feces of 1 *P. obsoletus* that originated in central Missouri but was owned and housed by the Cheyenne Mountain Zoological Park in Colorado. Upton and McAllister (1990) later reported *C. duszynskii* in 1/7 (14%) *P. guttatus* and in 1/4 (25%) *P. obsoletus* in Texas; McAllister et al. (1995; 2011) found it in 2/2 *P. emoryi* in Oklahoma and in 2/8 (25%) from Texas, in 1/3 (33%) *P. obsoletus* from Texas, and in 1/1 *L. calligaster* from Arkansas; McAllister et al. (2011) reported it in 3/3 *L. calligaster* from Arkansas (2/2) and Oklahoma (1/1), in 1/2 (50%) *L. holbrooki* from Arkansas, and in 1/6 (17%) *L. triangulum* from Arkansas; Upton et al. (1994) found it in 1/3 (33%) *M. flagellum* in Arkansas; and Modrý et al. (2005) found it in 3/3 (100%) *P. guttatus* imported into the Czech Republic from Florida, USA.

Sporulation: Exogenous. Oocysts were passed unsporulated or semisporulated and completed sporulation after 1 week in 2.5% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution at 27–30°C.

Remarks: Upton et al. (1990) said there were 17 *Caryospora* species known from reptiles when they described

the oocysts of *C. duszynskii* and that 8 species somewhat resembled their oocysts: *C. bengalensis*, *C. brasiliensis*, *C. demansiae*, *C. dendrelaphis*, *C. hermae*, *C. lampropeltis*, *C. legeri*, and *C. psammophis*. All of these were dismissed by them as different species because of various combinations of differences in oocyst and/or sporocyst sizes, structures of the oocyst wall, and size and shapes of SB, SSB, PG, SR, or SZs.

Lindsay, Sundermann and Blagburn (1988) watched *C. duszynskii* SZs penetrate human fetal lung cell cultures and observed them for 29 days. At 3 DPI, host cells lost their normal fibroblastlike shape and became ellipsoidal in shape, resembling caryocysts. Sporozoites remained viable from 3 to 29 DPI, as evidenced by motility of extracellular SZs in infected human fetal lung cell cultures. These results suggested to Lindsay, Sundermann and Blagburn (1988) that some *Carayospora* species may form caryocysts in secondary hosts without undergoing sexual or asexual multiplication in these hosts.

Upton et al. (1984a) and Matuschka (1986b) said that oocysts from snake feces were not infectious for mice. However, Modrý et al. (2005) used oocysts recovered from naturally infected *P. guttatus* from Florida, USA, to infect 2 mouse strains, BALB/c and Crl:CD–1(ICR)BR, *per os* with 50,000 sporulated oocysts. Mice were fed to 2 captive-born, coccidia-free *P. guttatus*. Both snakes discharged *C. duszynskii* oocysts in their feces on 18 and 28 DPI and shed oocysts continuously through 230 and 135 DPI, respectively, when their experiments ended. No parasitic stages or lesions could be found in the mice upon histological examination of their tissues. These experiments suggested that rodents can serve as paratenic hosts for *C. duszynskii*.

Caryospora epicrati Lainson, Nascimento and Shaw, 1991, emended Modrý, 1998

Synonym: Caryospora epicratesi Lainson, Nascimento and Shaw, 1991.

Type host: Epicrates cencheria (L., 1758), rainbow boa (Boidae).

Other hosts: None to date.

Type locality: Brazil: Rondônia, near the area of the hydroelectric dam "Samuel" (8°45'S, 63°28'W).

Sporulated oocyst: Spheroidal (18%) to predominantly subspheroidal (82%); number of walls: 2, ~1.5 thick; wall characteristics: outer is thicker, striated, and ~2/3rds of total; inner, smooth, nonstriated, ~0.5 thick; L × W (N = 50): 22.9 × 21.4 (19–25 × 17.5–22.5); L/W ratio: 1.1 (1.0–1.2); M, OR: both absent; PG: present, ~2.3 × 2.0, most frequently seen adhering to the sporocyst wall (67%) rather than to the oocyst wall (33%) as in other caryosporans.

Sporocyst and sporozoites: Broadly ellipsoidal; L × W (N = 50): 17.6 × 12.5 (16–19 × 11–12.5); L/W ratio: 1.4 (1.3–1.5); SB, SSB, SR: all present; SB and SSB: together forming a conspicuous stopperlike structure; SR: a central compact mass of large globules surrounded by the SZs like the staves of a barrel; SZ: each with both an anterior and a posterior RB.

Prevalence: Found in 1 *E. cencheria* examined by Lainson et al. (1991); they looked at the feces of "a number of snakes from Amazonia Brazil" when they described this species but didn't record the number of snakes infected with *C. epicrati*. Modrý (1998) said he found similar oocysts in 1 *E. cencheria* from Peru.

Sporulation: Exogenous, but the exact amount of time (and temperature) needed to sporulate is unknown.

Remarks: Frank (1985) published a photomicrograph that may represent this species. The most unique feature about *C. epicrati* is the PG that adheres to the sporocyst wall rather than the oocyst wall most of the time (Lainson et al., 1991). Modrý (1998) infected SCID mice with oocysts of this species but found no infection in histological sections. Modrý (1998), in his PhD dissertation, wrote that "According to the international rules of zoological nomenclature and Latin grammar, the specific name of this species should be corrected. It is evidently made as a genitive of the host generic name *Epicrates*. The right form of this name (which is masculinum) must be *epicrati* (p. 31)," and he promised to publish such a correction in the future. This creates a conundrum because I can find no record of such a published correction. Since dissertations are not considered peer-reviewed publications, this emendation from Modrý's dissertation (1998) appears to violate the "Criteria to be met" section (8.1) of article 8, "What constitutes published work," in chapter 3 of the *International Code of Zoological Nomenclature* (Ride et al., 1999, p. 6). Nonetheless, Modrý's corrected spelling has been picked up in the parasitological literature, and it should not be changed at this point.

Caryospora gracilis Upton, McAllister, Trauth and Bibb, 1992

Type host: Tantilla gracilis Baird and Girard, 1853, flathead snake (Colubridae).

Other hosts: None to date.

Type locality: USA: Texas, Hood County, 17.5 km SE of Granbury off of FM 2174.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, ~2.0 thick; wall characteristics: outer surface moderately pitted, ~1.0–1.4 thick; inner wall, smooth, ~0.6 thick; L × W (N = 30): 23.7 × 22.5 (21–25 × 21–24); L/W ratio: 1.1 (1.0–1.2); M: absent; OR: present, consisting of 1 to several masses of debris (?); PG: present, seen adhering to the inner surface of the oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W (N = 20): 17.1 × 12.7 (15–18 × 11–13.5); L/W ratio: 1.3 (1.3–1.4); SB, SSB, SR: all present; SB and SSB: both small, ~1.0 high × 2.5 wide; SR: L × W (N = 20): 13.9 × 6.5 (12–15 × 6–7), consisting of many granules in a compact cylindrical mass that runs the length of the sporocyst; SZ: elongate, 14.4 × 3.1 (13.5–15 × 2.5–3.5), with an anterior RB, 3.0 × 2.8 (2.5–4 × 2.5–3), and spheroidal posterior RB, ~2.4 (2–3), and with a N visible between RBs.

Prevalence: Upton, McAllister, et al. (1992) found this species in 4/12 (33%) specimens of the type host they examined (3 from Texas, 1 from Arkansas, USA).

Sporulation: Exogenous. All oocysts were passed unsporulated and attained full sporulation within 10 days maintained at 23°C.

Remarks: Oocysts of *C. gracilis* are unusual because they possess an OR, which most caryosporans do not, in addition to a very large, compact, cylindroidal SR.

***Caryospora guatemalensis* Seville, Asmundsson and Campbell, 2005**

Type host: Lampropeltis triangulum (Lacépède, 1789), Scarlet kingsnake (Colubridae).

Other hosts: None.

Type locality: Guatemala: Izabal, Morales, Sierra de Caral, Finca San Silvestre; no geographic coordinates were available.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, ~1.9 thick; wall characteristics: outer, yellow-brown, pitted, ~3/4 of total thickness; L × W (N = 11): 23.9 × 23.2 (20–27 × 20–26); L/W ratio: 1.0; M, OR: both absent; PG: 1, large, RB, adjacent to inner surface of the oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W: 14.4 × 10.6 (13–18 × 9–13); L/W ratio: 1.4; SB: nipple-like, SSB: large globular body, wider than SB; SR: a compact mass of granules with a few disbursed small granules; SZ: sausage-shaped, curled around central SR; RB, N: not observed.

Prevalence: Seville et al. (2005) discovered this species in 1/2 (50%) specimens of the type host they examined.

Sporulation: Unknown. Oocysts sporulated in the field.

Remarks: One line drawing and 3 photomicrographs were presented to support the description of this species. This form is similar in many respects to *C. lampropeltis*, originally described by Anderson et al. (1968) in *L. calligaster* from Illinois (USA) and later found in *L. getula* from Texas and in *L. triangulum* from Arkansas (McAllister et al., 1995). The argument regarding the separation of the oocysts of these forms from each other is weak (see Seville et al., 2005, p.1456, "Remarks"), and I believe they all represent the same species. This would make *C. guatemalensis* a junior subjective synonym of *C. lampropeltis*.

***Caryospora hermae* Bray, 1960**

Type host: Psammophis phillipsii Hallowell, 1844 (syn. *P. sibilans phillipsi* Loveridge, 1840), hissing, olive, or western sand snake (Psammophiidae).

Other hosts: Boaedon fuliginosus (Boie, 1827), African or brown house snake (Lamprophiidae); *Psammophis sibilans* (L., 1758), striped or hissing sand snake (Psammophiidae) (Norton and Pierce, 1985).

Type locality: Liberia, presumably near Harbel.

Sporulated oocyst: Subspheroidal; number of walls: 2; wall characteristics: colorless, smooth; L × W: 22.3 × 20.6 (21–24 × 20–22); L/W ratio: 1.1; M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal (line drawing); L × W: 16.5 × 12.6 (16–17 × 12–13); L/W ratio: 1.3; SB: present; SSB: may or may not be present, as it is not mentioned in the description nor is it included in the line drawing; SR: scattered granules; SZ: small, sausage-shaped (line drawing), surrounding the SR granules.

Prevalence: Bray (1960) examined 4 adult and 1 juvenile sand snakes, and only the juvenile (1/5, 20%) was passing oocysts of 3 caryosporan species, all of which he described as new.

Sporulation: Unknown.

Remarks: Bray (1960) fixed a piece of tissue of the intestine of the juvenile snake that was passing oocysts and said, "the coccidia were traced up the intestine and a piece of intestine at the point of the cessation of oocyst production was excised … and fixed." He then studied stained tissue sections of that piece of intestine and made (very primitive) line drawings of what he identified as meronts and micro- and macrogametocytes. He attributed various of these stages to large, medium, and small oocysts that he assigned to 3 different "new" species, *C. psammophi*, *C. hermae*, and *C. weyerae*, respectively. However, he never explained how he was able to distinguish endogenous stages of 1 *Caryospora* species from the other 2 when none of the endogenous stages he saw were known *a priori*. In other words, with 3 (?) species undergoing endogenous development at the same time, and in the same part of the intestine, how did Bray (1960) determine which stages went with which oocysts? Oocysts of these 3 species may be a continuum of sizes of a single species. It is also possible that this species may be a junior synonym of *C. legeri* Hoare (1933), which has similar oocysts.

Norton and Pierce (1985) surveyed snakes for parasites from Balmoral, Zambia (15°33′S, 28°12′S) and found caryosporan oocysts in 1/1 *B. fuglinosus* and in 2/3 (67%) *P. sibilans*. Their sporulated oocysts all were similar in structure but represented 3 distinct size classes (their Table 1, p. 61), large, medium, and small, that they believed represented the 3 similar species identified and named by Bray

(1960) as *C. psammophi*, *C. hermae*, and *C. weyerae,* respectively. Only *B. fuglinosus* had all 3 morphotypes in its feces while both infected *P. sibilans* shed the large and medium-sized oocysts but not those that were small (= *C. weyerae*?). Medium-sized oocysts of Norton and Pierce (1985) were 21.9 × 20.3 (18–26 × 18–23), and sporocysts were 15.4 × 11.6 (14–17 × 11–13) in *B. fuglinosus*; in *P. sibilans* #1, oocysts were 22.3 × 21.4 (19–24 × 18–23), and sporocysts were 16.0 × 12.4 (13–18 × 11–13); and in *P. sibilans* #2, oocysts were 21.1 × 19.0 (19–22 × 16–20), but sporocysts were not measured.

Hoare (1933) gave a very modest and inadequate description of *C. legeri* and said its oocysts ranged from 21–30 × 19–26, with sporocysts 16–19 × 11–14. This led Norton and Pierce (1985) to suggest that *C. hermae* may be a synonym of *C. legeri*, a suggestion they qualified by saying, "A wider range of samples from African ophidians should be examined to determine the host range of their Caryosporan parasites and to confirm the validity" (p. 61) of the 4 caryosporans of Hoare (1933) and Bray (1960).

Finally, Norton and Pierce (1985) fed sporulated oocysts (532 days old) from *B. fuglinosus* and oocysts from each of the two *P. sibilans* (357, 268 days old) to coccidia-free white mice; mouse tissues were examined 14 and 33 DPI by touch smears made from their intestine, kidney, liver, lymph nodes, diaphragm, heart, tongue, muscle, and brain, but no developmental stages were seen.

Caryospora heterodermus Upton, Freed and Freed, 1992

Type host: Philothamnus heterodermus Hallowell, 1857, emerald or variable green snake (Colubridae).

Other hosts: None to date.

Type locality: Africa: Cameroon, Southwest Province, Buea.

Sporulated oocyst: Spheroidal; number of walls: 2, 1.5–2.0 thick; wall characteristics: outer, ~0.8–1.4, lightly to moderately pitted; inner layer, 0.4–0.6 thick, smooth; L × W (N = 40): 20.0 (15–22.5); L/W ratio: 1.0; M: absent; OR: present, either scattered or a small, compact mass, L × W (N = 10): 2.1 × 1.4 (1–4 × 1–2.5); PG: spheroidal, 1.9 (1.5–2.5), and is adjacent to inner surface of the oocyst wall (line drawing).

Sporocyst and sporozoites: Ovoidal; L × W (N = 20): 16.3 × 11.6 (12–18 × 10–13); L/W ratio: 1.4 (1.2–1.5); SB: present, L × W (N = 20): 1.0 high × 3.8 wide (1–1.5 × 3–5); SSB: present, L × W (N = 20): 1.4 high × 4.1 wide (1–2 × 3–5); SR: many granules in a compact mass, L × W (N = 20): 11.2 × 5.0 (6.5–14 × 4–6.5); SZ: elongate, banana-shaped, L × W (N = 20): 14.5 × 3.2 (10.5–17 × 3–3.5); SZ: each containing 2 RBs with a N between them.

Prevalence: Upton, Freed and Freed (1992) discovered this species in the feces of the only specimen of the type host they examined.

Sporulation: Exogenous. Oocysts were passed unsporulated and sporulated within 10 days at 23°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$).

Remarks: Although *C. heterodermus* has sporulated oocysts similar to those of more than a dozen previously described *Caryospora* species from snakes, it is unique in having both a PG and an OR that most others lack. However, it has not been found again since its initial description.

Caryospora japonicum Matubayashi, 1936

Type host: Rhabdophis tigrinus (Boie, 1826) (syns. *Natrix tigrina* [Boie, 1826]; *Natrix tigrine* Stejneger, 1907), Yamakagashi snake of Japan or tiger keelback (Colubridae).

Other hosts: None to date.

Type locality: Japan: Tiba Prefecture, caught in Hota.

Sporulated oocyst: Mostly spheroidal to slightly subspheroidal; number of walls: 2; wall characteristics: outer layer thinner than inner layer; larger oocysts appear light brown while smaller forms are colorless; L × W (N = 250): 18.6 (15–22); L/W ratio: 1.0; M, OR: both absent; PG: described as present, not pictured in line drawings (Matubayashi, 1937, Figs. 24–32, pp. 271, 273), but can be seen in his only photomicrograph of *C. japonicum* (1937, Fig. 36, p. 275).

Sporocyst and sporozoites: Ovoidal; L × W: no measurements given, only that the length of the sporocyst "almost coincides (with) the inner diameter of the oocyst wall (Matubayashi, 1936, p. 1729); SB: present; SSB: present initially, and said to disappear during sporulation, but it was probably just obscured by the developed SZs; SR: large bunch of granules surrounded by SZs; SZ: banana-shaped, each containing 3 large RBs, 1 at each extremity and 1 in the center of the SZ.

Prevalence: Matubayasi (1937) reported this species in 11/50 (22%) *R. tigrinus* from which he collected fecal material.

Sporulation: Exogenous. Oocysts sporulated in 3 days at 25°C when kept in 0.5–1.0% chromic acid.

Remarks: Matubayasi (1936) published his description and naming of *C. japonicum* in Japanese. Realizing Japanese was not a mainstream language in science, he published his "new species" description and name a year later in English (Matubayasi, 1937) using the same line drawings and photomicrographs. This species has not been found again since its original description(s).

***Caryospora jararacae* (Carini, 1939) Lainson, Nascimento and Shaw, 1991**

Synonym: syn. *Caryospora jaracae* Carini, 1939 *lapsus calami*.

Type host: Bothrops jararaca (Wied–Neuwied, 1824), jararaca (Viperidae).

Other hosts: Bothrops atrox (L., 1758), fer-de-lance (Lainson et al., 1991) (Viperidae); *Bothriechis lateralis* Peters, 1862, coffee palm viper (Viperidae).

Type locality: Brazil: São Paulo State, Mogi das Cruzes (23°31'S, 46°11'W).

Sporulated oocyst: Predominantly spheroidal (86%) to subspheroidal (14%); number of walls: 1, ~0.7 thick; wall characteristics: smooth, colorless, with no striations; L × W (N = 50): 13.0 × 13.0 (12.5–14 × 12.5–14); L/W ratio: 1.0 (1.0–1.1); M, OR: both absent; PG: present, 1.2 × 2.0, usually seen adhering to the inner oocyst wall.

Sporocyst and sporozoites: Broadly ellipsoidal; L × W (N = 50): 10.0 × 8.7 (9–11 × 7.5–9); L/W ratio: 1.1 (1.1–1.3); SB, SSB, SR: all present; SB and SSB: together forming an inconspicuous stopperlike structure; SR: about 20 spheroidal granules surrounded by the SZ that are arranged longitudinally; SZ: each with both an anterior and a posterior RB and with delicate transverse cytoplasmic corrugations (?).

Prevalence: No information on how many *B. jararaca* were examined by Carini (1939); Lainson et al. (1991) found it in 1/19 (5%) *B. atrox* they collected in Amazonas State, Brazil (1°55'S, 59°28'W).

Sporulation: Exogenous, but the exact amount of time (and temperature) needed to sporulate is unknown.

Remarks: Carini (1939) misspelled the name of his new species in the legend of his line drawing as *jaracae*, and his modest description was primitive and inadequate by current standards, but he did provide a line drawing. The mensural descriptives of oocysts and sporocysts (above) are taken from Lainson et al. (1991), who included a PG, SSB, and the peculiar striations of the SZs missing in Carini's description; they did note that these structures are difficult to see in an oocyst as small as that of *C. jararacae*.

***Caryospora kalimantanensis* Modrý and Koudela, 1997**

Type host: Boiga dendrophila (Boie, 1827), mangrove or gold-ringed cat snake (Colubridae).

Other hosts: None to date.

Type locality: Malaysia: State of Sabah, Kalimantan lowland rainforest area, 350 m.

Sporulated oocyst: Spheroidal; number of walls: 2, ~1.5 thick; wall characteristics: outer layer pitted, 2/3rds of total thickness; L × W (N = 30): 18.7 (17–20); L/W ratio: 1.0; M, OR: both absent; PG: 2.0 wide, present in about half of the sporulated oocysts measured and usually seen near the oocyst wall (line drawings, photomicrographs).

Sporocyst and sporozoites: Ovoidal to ellipsoidal; L × W (N = 30): 14.5 × 10.5 (13–15.5 × 10–11); L/W ratio: 1.4 (1.2–1.5); SB, SSB, SR: all present; SB: domelike, 1.0–1.5 high × 2.0 wide; SSB: 1.0–1.5 high × 2.0–2.5 wide; SR: small irregular-sized granules scattered among SZs; SZ: sausage-shaped (line drawing), 11.8 × 2.8 (10–13.5 × 2–3.5) with both an anterior and a posterior RB and a visible N that lies between RBs.

Prevalence: Found in the only specimen of the type host available for examination. The snake, collected in Kalimantan, was imported into the Czech Republic, where it was housed alone in a private collection.

Sporulation: Unknown but probably exogenous; 24 hours after fecal collection, when they were examined for the first time, about 90% of the oocysts were fully sporulated.

Remarks: This is the first caryosporan described from the host genus *Boiga*. Sizewise it resembles at least 9 other caryosporans, and Modrý and Koudela (1997) discuss the structural and size differences that helped them decide that this was a new species in addition to its host and geographical distinctions.

***Caryospora lampropeltis* Anderson, Duszynski and Marquardt, 1968**

Type host: Lampropeltis calligaster (Harlan, 1827), prairie kingsnake (Colubridae).

Other hosts: Heterodon platirhinos Letreille, 1801, eastern hognose snake; *Lampropeltis holbrooki* Stejneger, 1902, speckled kingsnake; *Lampropeltis triangulum* (Lacépède, 1789), eastern milksnake (all Colubridae).

Type locality: USA: Illinois, Jackson County.

Sporulated oocyst: Spheroidal; number of walls: 2, ~1.0 thick; wall characteristics: outer layer finely pitted, 1/2 of total thickness; L × W (N = 50): 23.3 (20–25); L/W ratio: 1.0; M, OR: both absent; PG: present, ~1–2 wide, closely associated with inner layer of oocyst wall (line drawing, photomicrograph).

Sporocyst and sporozoites: Ovoidal; L × W (N = 50): 17.1 × 12.3 (15–19 × 11–13); L/W ratio: 1.4 (1.25–1.6); SB, SSB, SR: all present; SB: prominent, nipple-like; SSB: present but usually obscured by SZ; SR: compact mass of small granules surrounded by SZs; SZ: banana-shaped, slightly pointed at 1 end, L × W: 13 × 3, with both an anterior and a posterior RB and a visible N that lies between RBs; SZs surround and enclose the SR.

Prevalence: Anderson et al. (1968) found and described this species in the only specimen of the type host they examined. McAllister et al. (1995) reported it again in 1/1

L. holbrooki from Texas (originally reported as *L. getula*; see McAllister et al., 2015, p. 153), and McAllister et al. (2015) found and redescribed *C. lampropentis* in 1/4 (25%) *H. platirhinos* collected in Arkansas (in 1/2) and Oklahoma (0/2).

Sporulation: Exogenous. Oocysts are passed unsporulated or nearly sporulated and are fully sporulated after 1 week in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution (McAllister et al., 2015).

Remarks: In their redescription of the sporulated oocysts, McAllister et al. (2015) said the spheroidal/subspheroidal oocysts were L × W (N = 13): 23.5 × 22.8 (21–26 × 20–26); L/W ratio: 1.0 (1.0–1.1) with ovoidal sporocysts, L × W (N = 13): 16.8 × 12.8 (16–18 × 11–14); L/W ratio: 1.3 (1.2–1.5); they noted only slight differences in the SR between the 2 descriptions. *Caryospora lampropeltis* has been compared to a few other caryosporans from snakes like *C. brasiliensis*, *C. guatemalensis*, and *C. duszynskii,* but there are sufficient differences both in oocyst and sporocyst structures and geographic localities to conclude they are different species for now, until molecular evidence can prove otherwise.

***Caryospora legeri* Hoare, 1933**

Synonym: Caryospora legeti Matubayashi, 1937 (*lapsus*).
Type host: Psammophis sibilans (L., 1758), Egyptian hissing sand snake (Psammophiidae).

Other hosts: None to date.

Type locality: Uganda: Entebbe.

Sporulated oocyst: Subspheroidal; number of walls: 2; wall characteristics: thick, greyish-colored wall; L × W: 21–30 × 19–26; L/W ratio: unknown, means not given; M: a minute, funnel-shaped hole was sometimes seen in the oocyst wall but not included in the line drawings provided (Hoare, 1933, Figs. 11, 12, p. 361); OR, PG: both absent.

Sporocyst and sporozoites: Ovoidal; L × W: 16–19 × 11–14; L/W ratio: unknown, means not given; SB, SSB, SR: all present; SB: prominent, globelike knob; SSB: present, globelike (line drawing) but not as wide as SB (Hoare, 1933, Fig. 12, p. 361); SR: compact mass of small granules surrounded by SZs; SZ: spindle-shaped, each ~11 long, surrounding and enclosing the SR like the staves of a barrel; 1 central RB in each SZ (Fig. 12).

Prevalence: This species was found in 2/3 (67%) specimens of the type host examined by Hoare (1933).

Sporulation: Exogenous. Oocysts passed unsporulated and become fully sporulated in ~48 hours at room temperature when placed in 1% chromic acid.

Remarks: Hoare spent 1927–1929 in Uganda, during which he examined about 400 vertebrates for protozoa, only 11 of which were found to harbor coccidia (Hoare, 1933). Hoare (1933) fixed the intestine of one of the snakes passing oocysts and found meronts and gametes within the epithelial villi of the small intestine. Upton et al. (1986) suggested that the minute M reported on some of the oocysts may be oocyst wall pitting such as described by Cannon (1967) for *C. demansiae*. Dollfus (1961) said that *C. legeri* was a parasite of *Vipera apis*, but I agree with Upton et al. (1986) that Dollfus's parasite was likely *C. simplex*.

***Caryospora maculatus* Upton, Freed and Freed, 1992**

Type host: Causus maculatus (Hallowell, 1842), spotted night adder (Viperidae).

Other hosts: None to date.

Type locality: Africa: Cameroon, Southwest Province, 1 km south of Mbalangi.

Sporulated oocyst: Spheroidal; number of walls: 2, ~1.0 thick; wall characteristics: both layers smooth, each ~0.4–0.5 thick; L × W (N = 40): 12.1 (11–13); L/W ratio: 1.0; M, OR: both absent; PG: present in only 5/40 (12.5%) oocysts examined and measured.

Sporocyst and sporozoites: Ovoidal; L × W (N = 20): 10.1 × 7.9 (9.5–11 × 7.5–8.5); L/W ratio: 1.3 (1.2–1.4); SB: present, as a thickening of 1 end of the sporocyst; SSB: present, small and inconspicuous; SR: small cluster of granules with a central globule, 2–2.5 wide; SZ: banana-shaped (line drawing), L × W (N = 12): 8.4 × 2.0 (7–9.5 × 1.5–2.5), each containing 2 small RBs with a N between them and the anterior ends indicate light striations (line drawing).

Prevalence: Upton, Freed and Freed (1992) discovered this species in the feces of 1/2 (50%) of the specimens of the type host they examined.

Sporulation: Exogenous. Oocysts were passed unsporulated and sporulated within 10 days at 23°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$).

Remarks: Caryospora maculatus is among the smallest of all serpentine caryosporans known to date. Only *C. minuta* from a snake in Madagascar (Upton, Freed, et al., 1990) is smaller.

***Caryospora madagascariensis* Upton, Freed, Burdick and McAllister, 1990**

Type host: Madagascaropis colubrinus (Schlegel, 1837), Madagascar cat-eye snake (Colubridae).

Other hosts: Mimophis mahfalensis (Grandidier, 1867), Malagasy colubrid (Colubridae).

Type locality: Madagascar.

Sporulated oocyst: Spheroidal; number of walls: 2, 1.4–2.4 thick; wall characteristics: outer, relatively smooth, ~4/5 of total thickness (line drawing); L × W (N = 25): 26.2 × 24.4 (22–30 × 21–27); L/W ratio: 1.1 (1.0–1.1); M, OR: both absent; PG: 1 present, 2.5 wide, usually associated with inner surface of oocyst wall (line drawing).

Sporocyst and sporozoites: Ellipsoidal; L × W (N = 25): 18.2 × 13.3 (16–20 × 12–15); L/W ratio: 1.4 (1.2–1.5); SB, SSB, SR: all present; SB: domelike, 1.8 high × 2.9 wide (1–2 × 2–4); SSB: 1.7 high × 3.4 wide (1–2 × 3–4); SR: large granules scattered among SZs; SZ: vermiform, 15.7 × 3.3 (14–17 × 3–4); each with prominent anterior transverse striations and 2–3 RBs.

Prevalence: Found in 3/4 (75%) specimens of the type hosts examined and in 1/6 (17%) *M. mahfalensis* from Madagascar.

Sporulation: Unknown, oocysts sporulated in the field before they reached the lab to be examined.

Remarks: Line drawing and 2 photomicrographs were included to help support the species description. Upton, Freed, et al. (1990) stated that the oocysts of this form are most similar to those of *C. legeri* from *Psammophis sibilans* in Uganda but has longer sporocysts, and bigger oocysts in addition to the host and geographic differences.

***Caryospora masticophis* Upton, McAllister and Trauth, 1994**

Type host: Masticophis flagellum flagellum (Shaw, 1837), eastern coachwhip (Colubridae).

Other hosts: Coluber constrictor priapus Dunn and Wood, 1939, Southern black racer (Colubridae).

Type locality: USA: Arkansas, Saline County, 4.8 km south of Lake Maumelle at Moss Mountain.

Sporulated oocyst: Spheroidal or rarely subspheroidal; number of walls: 2, ~1.0 thick; wall characteristics: smooth, both layers of equal thickness; L × W (N = 25): 13.6 × 13.5 (13–14 × 13–14); L/W ratio: 1.0 (1.0–1.1); M, OR: both absent; PG: 1 present, usually attached to inner surface of oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W (N = 15): 10.9 × 8.1 (10–11 × 8–9); L/W ratio: 1.35 (1.3–1.4); SB, SSB, SR: all present; SB: 1.0 high × 2.0–2.5 wide; SSB: 1.5 high × 2.5 wide; SR: a few granules scattered among SZs; SZ: banana-shaped (line drawing), L × W (N = 15): 9.3 × 2.2 (9–11 × 2–2.4), sometimes with anterior transverse striations and 1–2 RBs; N slightly posterior to midpoint of body.

Prevalence: Found in 1/3 (33%) specimens of the type host examined and in 1/10 (10%) *C. c. priapus*.

Sporulation: Unknown, oocysts sporulated in the field before they reached the lab to be examined.

Remarks: Upton et al. (1994) said the oocysts they isolated from both the type host, *M. f. flagellum*, and from *C. c. priapus*, were morphologically identical and, thus, considered them to be the same species. The sporulated oocysts from *C. c. priapus* were, L × W (N = 25): 13.8 (13–14) with sporocysts, L × W (N = 15): 10.9 × 8.1 (10–11 × 8–9) with L/W ratio, 1.3 (1.2–1.4).

***Caryospora matatu* Modrý, Šlapeta and Koudela, 2002**

Type host: Atheris ceratophora Werner, 1896 (syn. *Atheris ceratophorus* Werner, 1895) of Modrý et al. (2002), horned bush viper (Viperidae).

Other hosts: None to date.

Type locality: Tanzania: Usambara Mountains.

Sporulated oocyst: Spheroidal to slightly subspheroidal; number of walls: 2, 1.5 thick; wall characteristics: outer layer brownish, distinctly pitted such that various types of debris tend to stick to the surface; inner layer, thin, < 0.5; L × W (N = 30): 19.8 (16–23); L/W ratio: 1.0; M, OR: both absent, although in some oocysts 2–5 small granules occur; PG: only 1, ~1.0 wide, close to the inner oocyst wall.

Sporocyst and sporozoites: Ellipsoidal; L × W (N = 30): 15.6 × 10.1 (12.5–17 × 8–12); L/W ratio: 1.5 (1.4–1.7); SB, SSB, SR: all present; SB: domelike, 1.0 high × 2–3 wide; SSB: 2.0 high × 4.0 wide but indistinguishable in some sporocysts where it presents as a distinct halo between SB and SZ; SR: numerous small granules scattered among SZs; SZ: vermiform with a lightly striated surface and both an anterior and a posterior RB and a N between them, although these are often not visible.

Prevalence: Found in 1/4 (25%) specimens of the type host examined by Modrý et al. (2002).

Sporulation: Exogenous. Sporulation occurred within 5 days when maintained at 19–21°C.

Remarks: Prior to their paper (Modrý et al., 2002), there were 8 *Caryospora* species described from snakes from sub-Saharan Africa, but only *C. maculatus* from *Causus maculatus* (Upton, Freed and Freed, 1992) was found in an African viperid. The oocysts of other caryosporans from African snakes are easily distinguished from those of *C. matatu* by multiple features of oocyst size and structures. The oocysts of *C. maculatus* are much smaller, have a smooth wall, and lack a PG, and the SB/SSB complex is very different. Modrý et al. (2002) provided a useful table (Table 1, p. 343) to distinguish oocysts of *C. matatu* from other caryosporans in viperids worldwide.

***Caryospora maxima* Modrý, Koudela, Al-Oran and Amr, 1999**

Type host: Psammophis schokari (Forskål, 1775), Forskål's sand snake (Psammophiidae).

Other hosts: Echis coloratus Günther, 1878, Palestine saw-scaled viper (Viperidae).

Type locality: Jordan: Safawi (32°12'N, 37°10'E).

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, ~2 thick; wall characteristics: outer layer brownish, 3/4 of total thickness; L × W: 43.0 × 42.1 (40–46 × 40–44); L/W ratio: 1.0; M, OR, PG: all absent.

Sporocyst and sporozoites: Broadly ellipsoidal; L × W: 21.3 × 16.3 (21–22 × 16–17); L/W ratio: 1.3; SB, SSB, SR: all present; SB: knoblike, 1.0 high × 3.0 wide; SSB: a homogeneous globule, 4.0 high × 4.5 wide; SR: compact mass of granules lying centrally between SZs; SZ: banana-shaped (line drawing) with both an anterior and a posterior RB and a visible N between RBs.

Prevalence: Found in 1/3 (33%) specimen of the type host examined by Modrý et al. (1999). Alyousif et al. (2004) reported finding oocysts identical to *C. maxima* in 3/26 (11.5%) saw-scaled vipers collected in the Gazan area of Saudia Arabia.

Sporulation: Exogenous. However, when intestinal contents were examined when 15 days old, 100% of the oocysts were sporulated.

Remarks: This was the first *Caryospora* sp. found in *P. schokari* and was easily distinguished from other caryosporans in snakes by the large size of its oocysts. It is also much larger than the 4 other *Caryospora* species described from the genus *Psammophis* (*C. hermae, C. legeri, C. psammophi, C. weyerae*) by Bray (1960), Hoare (1933) and Norton and Pierce (1985). The oocysts of *C. maxima* also are larger than the other largest known species, *C. cheloniae*, described from the green sea turtle, *Chelonia mydas* (Leibovitz et al., 1978), which has oocysts 33–40 wide. Modrý (1998) and Modrý et al. (1999) also found numerous extranuclear stages of gamogony in the enterocytes of the small intestine but did not describe them.

Alyousif et al. (2004) measured oocysts and sporocysts from a viper, *E. coloratus*, that were nearly identical to measurements in Modrý et al.'s (1999) original description of *C. maxima*: oocyst L × W (N = 50): 42.8 × 41.2 (40–45 × 40–44); L/W ratio: 1.0 (1.0–1.1); M, OR: both absent but a PG was present in some oocysts; sporocysts: L × W (N = 50): 22.1 × 16.8 (21–23 × 15.5–17); L/W ratio: 1.3 (1.2–1.5); SB, SSB, SR: all present; SB: domelike, 1.3 high × 3.4 wide; SSB: 3.7 high × 4.5 wide; SR: compact mass of granules lying centrally between SZs; SZ: banana-shaped with both an anterior and a posterior RB and a visible N that lies between RBs.

Caryospora mayorum Seville, Asmundsson and Campbell, 2005

Type host: Conophis lineatus (Duméril, Bibron and Duméril, 1854), road guarder snake (Colubridae).

Other hosts: None.

Type locality: Guatemala: Zacapa, San Vicente, Area El Arenal (14°10.05'N, 90°58.01'W).

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, 2.4 thick; wall characteristics: outer, yellow-brown, heavily pitted, ~3/4 of total thickness; L × W (N = 5): 25.6 × 24.4 (24–27 × 24–25); L/W ratio: 1.0; M, OR: both absent; PG: 1, large, refractile, adjacent to inner surface of the oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W: 16.3 × 11.9 (16–18 × 11–13); L/W ratio: 1.4; SB: large, nipple-like; SSB: large globular body, wider than SB; SR: a central mass of a few disbursed small granules; SZ: sausage-shaped, curled around granules of SR; RB, N: not observed.

Prevalence: Seville et al. (2005) discovered this species in 1/4 (25%) of the specimens of the type host they examined.

Sporulation: Unknown. Oocysts sporulated in the field.

Remarks: One line drawing and 3 photomicrographs were presented to support this species description. This is the second *Caryospora* species described from *Conophis*, but it is larger than *C. conophae* from the same host species, and it has a thicker oocyst wall and a much larger SB and SSB. It also is superficially similar to *C. duszynskii* described in *Elapha guttata* from Georgia (USA) by Upton et al. (1984a), but Seville et al. (2005) clearly point out their distinctive differences.

Caryospora micruri Lainson, Paiva do Nascimento and Shaw, 1991

Type host: Micrurus spixii spixii Schmidt and Walker, 1943, Amazonian coral snake (Elapidae).

Other hosts: None.

Type locality: Brazil: Rondônia, area of the hydroelectric dam "Samuel" (8°45'S, 63°28'W).

Sporulated oocyst: Mostly spheroidal (68%) to slightly subspheroidal (32%); number of walls: 1, ~0.6 thick; wall characteristics: smooth, colorless; L × W (N = 50): 16.1 × 16.0 (14–17.5 × 14–17.5); L/W ratio: 1.0 (1.0–1.1); M, OR: both absent; PG: 1, 2.5–1.2, usually adhering to inner surface of the oocyst wall.

Sporocyst and sporozoites: Broadly ellipsoidal; L × W: 13.7 × 10.2 (12.5–15 × 9–11); L/W ratio: 1.3 (1.2–1.4); SB, SSB: together form a stopperlike structure; SSB: about the same width as SB; SR: a central mass of small granules and larger globules (line drawing); SZ: sometimes arranged longitudinally to enclose SR and sometimes irregularly disposed; RB: both anterior and posterior bodies in each SZ.

Prevalence: Unknown.

Sporulation: Unknown.

Remarks: Lainson et al. (1991) looked at the feces of "a number of snakes from Amazonia Brazil" when they found this species, but they did not record its prevalence in the snakes they examined.

***Caryospora minuta* Upton, Freed, Burdick and McAllister, 1990**

Type host: Leioheterodon madagascariensis Duméril and Bibron, 1854, Madagascar hognose snake (Colubridae).

Other hosts: None to date.

Type locality: Madagascar.

Sporulated oocyst: Spheroidal; number of walls: 2, 0.8–1.2 thick; wall characteristics: smooth, both layers of equal thickness; L × W (N = 25): 11.6 (10–13); L/W ratio: 1.0; M, OR: both absent; PG: small, usually associated with inner surface of oocyst wall.

Sporocyst and sporozoites: Ellipsoidal; L × W (N = 25): 9.8 × 7.9 (8–11 × 7–9); L/W ratio: 1.2 (1.1–1.4); SB, SSB, SR: all present; SB: flat, 0.8 high × 2.4 wide (0.6–1.2 × 2–3); SSB: small, indistinct, 0.8–1.6 high × 2.4–3.2 wide; SR: 5–20 relatively large granules, 0.8–1.4 scattered among SZs; SZ: vermiform, 8.9 × 2.4 (8–10 × 2–3); each with prominent anterior transverse striations and 2 spheroidal to subspheroidal RBs.

Prevalence: Found in 1/2 (50%) specimens of the type host examined from Madagascar.

Sporulation: Unknown; oocysts sporulated in the field before they reached the lab to be examined.

Remarks: Line drawing and 2 photomicrographs were included to support the description of this species. This is the smallest *Caryospora* species described from snakes.

***Caryospora najadae* Matuschka, 1986a**

Type host: Platyceps najadum (Eichwald, 1831) (syn. *Coluber najadum* Schmidt, 1939), Dahl's whip snake (Colubridae).

Other hosts: None to date.

Type locality: Israel: near Haifa.

Sporulated oocyst: Spheroidal; number of walls: 2, ~1.5–2.0 thick; wall characteristics: smooth; L × W (N = 43): 31.9 (28–36); L/W ratio: 1.0; M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal; L × W (N = 43): 21.1 × 15.2 (20–22 × 14–16); L/W ratio: 1.4; SB, SSB, SR: all present; SB: 2.5 high × 2.5 wide; SSB: distinctly wider than SB, SR: described only as, "a cluster of several spherical bodies;" SZ: banana-shaped (photomicrograph), L × W: 19–21 × 2.0–2.5, arranged around the SR, and each SZ has a spheroidal anterior and posterior RB.

Prevalence: Found in the only specimen of the type host examined by Matuschka (1986a).

Sporulation: Exogenous. Oocysts became fully sporulated in ~72 hours in 2.5% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) when feces were at 21°C.

Remarks: So far, *C. najadae* has among the largest oocysts (but also see *C. psammophi* [Bray, 1960] and *C. maxima* [Modrý et al., 1999]) and sporocysts described from snakes. Its spheroidal oocysts also are larger than those of *C. colubris* (28–36 vs. 16–28), as are its sporocysts (14–16 × 20–22 vs. 10–15 × 13–19).

***Caryospora najae* Matuschka, 1982**

Type host: Naja nigricollis Reinhardt, 1843, black-necked spitting cobra (Elapidae).

Other hosts: None to date.

Type locality: East Africa.

Sporulated oocyst: Spheroidal; number of walls: 2, ~1.0 thick; wall characteristics: smooth, outer layer translucent, thicker than inner, darker layer; L × W: 15.1 (14–16); L/W ratio: 1.0; M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal; L × W: 11.2 × 8.8 (11–12 × 8–9); L/W ratio: 1.3; SB, SSB, SR: all present; SB: distinct at more pointed end of sporocyst; SSB: indistinct; SR: described only as "completely filling sporocyst"; SZ: banana-shaped, L × W: 13.5 (12.5–15.3) × 2.5 and arranged around the SR.

Prevalence: Found in 2/2 of the type hosts examined by Matuschka (1982).

Sporulation: Exogenous. Oocysts became fully sporulated in about 24–48 hours when feces were at 23°C.

Remarks: Matuschka (1982) noted that unsporulated oocysts were slightly smaller than were sporulated oocysts. He also killed 1 infected snake and fixed and examined its heart, kidney, liver, lung, muscle, and intestinal tissues. Endogenous developmental stages of merogony and gamogony were found above the N of epithelial cells in the third fifth of the small intestine, and various stages of endodyogeny were found in liver cells of the infected snake; merozoites found in the liver were L × W: 20–25 × 3.5–4.5. He also infected 2 NMRI-mice *per os* with 1×10^5 sporulated oocysts, killing 1 at 4 and the other at 8 weeks PI to look at lymph nodes, liver, lung, kidney, muscle, and spleen for tissue stages of the parasite. However, no parasite stages were found in either touch smears or tissue sections from the mice infected with sporulated oocysts. Upton et al. (1984a) and Matuschka (1982) said that oocysts from snake feces were not infectious for mice, suggesting that not all species of *Caryospora* have life cycles that use 2 hosts; on the other hand, it is possible that other species of vertebrates may serve as vectors. This was the first report of a *Caryospora* species from the spitting cobra.

***Caryospora olfersii* Viana, Winck, Coelho, Flausino and Duarte Rocha, 2013**

Type host: Philodryas olfersii (Lichtenstein, 1823), Lichtenstein's green racer (Colubridae).

Other hosts: None to date.

Type locality: Brazil: Rio de Janeiro State, São João da Barra municipality, Restinga de Grussaí (21°44′10.20″S, 41°01′53.39″W).

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 3, 1.4 (0.9–2.2) thick; wall characteristics: outer, smooth, colorless; middle, lightly striated; inner, thin; L ×

W (N = 72): 33.1 × 31.2 (27–39 × 22.5–38.5); L/W ratio: 1.1 (1.0–1.3); M, OR, PG: all absent.

Sporocyst and sporozoites: Ellipsoidal; L × W (N = 72): 22.9 × 17.4 (18–27 × 14–20); L/W ratio: 1.3 (1.1–1.6); SB, SSB, SR: all present; SB: nipple-like, 1.3 high × 3.2 wide; SSB: large, 1.7 high × 4.5 wide (4–6 × 1–3); SR: composed of granules of differing sizes that enclose the SZs.

Prevalence: Found in 1/2 (50%) specimen of the type host examined.

Sporulation: Unknown.

Remarks: Line drawing and 2 photomicrographs were included to support their determination of a new species. Viana et al. (2013, Table 1) compared the sporulated oocysts of this form to those of other *Caryospora* species in colubrid snakes known from South America at the time—*C. brasiliensis*, *C. carajasensis*, *C. paraensis*, and *C. pseusteisi* (from Carini, 1932, 1939; Lainson and Shaw, 1973; Lainson et al., 1991)—distinguishing its larger oocyst and sporocyst sizes and its three-layered oocyst wall from them.

Caryospora paraensis Lainson, Nascimento and Shaw, 1991

Type host: Oxyrhopus petola digitalis (Reuss, 1834), forest flame snake (Colubridae).

Other hosts: None to date.

Type locality: Brazil: Pará State, Serra dos Carajás (6°S, 50°18′W).

Sporulated oocyst: Spheroidal (76%) to subspheroidal (24%); number of walls: 1, ~1.0 thick; wall characteristics: smooth, colorless, no striations; L × W (N = 50): 17.3 × 17.0 (16–19 × 15–19); L/W ratio: 1.0 (1.0–1.3); M, OR: both absent; PG: present, ~2.0 × 1.2, usually adhering to inner oocyst wall.

Sporocyst and sporozoites: Broadly ellipsoidal; L × W (N = 50): 14.4 × 10.8 (14–16 × 10–12.5); L/W ratio: 1.3 (1.2–1.5); SB, SSB, SR: all present; SB: nipple- or stopper-like; SSB: about same width as SB, somewhat inconspicuous (line drawing); SR: a central compact mass of granules or irregularly scattered in sporocyst among SZs; SZ: 1–2 RBs in each.

Prevalence: Unknown.

Sporulation: Unknown.

Remarks: Lainson et al. (1991) looked at the feces of "a number of snakes from Amazonia Brazil" when they described this species but did not record the prevalence in *O. p. digitalis*.

Caryospora peruensis Upton, Freed and Freed, 1989

Type host: Xenoxybelis argenteus (Daudin, 1803) (syn. *Coluber argenteus* Daudin, 1803), striped sharp-nosed snake (Colubridae).

Other hosts: None to date.

Type locality: Peru: Ucayali District, 65 km ENE of Pucallpa.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, 2.6 thick; wall characteristics: outer layer ~1.8, heavily pitted; inner layer, ~0.8, smooth; L × W (N = 30): 28.5 × 26.3 (26–31 × 24–28); L/W ratio: 1.1 (1.0–1.2); M, OR: both absent; PG: 1, occasionally 2 present, usually adhering to inner oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W (N = 25): 19.5 × 13.6 (18–21 × 12–15); L/W ratio: 1.4 (1.3–1.6); SB, SSB, SR: all present; SB: caplike (line drawing), L × W (N = 15): 1.7 high × 4.4 wide (1.6–2.4 × 3–5); SSB: large homogeneous spheroid, L × W (N = 15): 3.1 high × 4.7 wide (2–4 × 4–5); SR: compact mass of granules surrounded by SZs; SZ: each with 2 large, mostly spheroidal RBs and a central N.

Prevalence: Found in 1/3 (33%) specimens of the type host examined.

Sporulation: Unknown. Oocysts were stored in vials in the field for up to 1 month before they could be examined.

Remarks: Only sporulated oocysts of *C. duszynskii* have oocysts similar to those of *C. peruensis*. Upton et al. (1989) felt that the oocysts of this species had generally larger dimensions, including larger oocysts and sporocysts, and the latter were longer (L/W 1.4 vs. 1.2). They also said the oocyst walls are thicker and more heavily pitted, and the SZ are longer.

Caryospora psammophi Bray, 1960

Type host: Psammophis phillipsii Hallowell, 1844 (syn. *P. sibilans phillipsi* Loveridge, 1840), hissing, olive, or western sand snake (Psammophiidae).

Other hosts: None.

Type locality: Liberia, presumably near Harbel.

Sporulated oocyst: Subspheroidal; number of walls: 2; wall characteristics: thin, yellow layers, the outer being finely and irregularly pitted; L × W: 29.1 × 26.8 (25–34 × 23–31); L/W ratio: 1.1; M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal (line drawing); L × W: 20.8 × 14.5 (19–23 × 13–16); L/W ratio: 1.4; SB: present (line drawing); SSB: may or may not be present, as it is not mentioned in the description nor is it included in the line drawing; SR: a central mass of small, scattered granules; SZ: small, sausage-shaped bodies, surrounding the SR granules; SZ: only 1 measured; it was 9 × 2.5.

Prevalence: Bray (1960) examined 4 adult and 1 juvenile sand snakes, and only the juvenile (1/5, 20%) was passing oocysts of 3 caryosporan species, all of which he described as new.

Sporulation: Unknown.

Remarks: Bray (1960) fixed a piece of intestine of the juvenile snake that was passing oocysts and said "the

coccidia were traced up the intestine, and a piece of intestine at the point of the cessation of oocyst production was excised . . . and fixed." He then studied stained tissue sections of that piece of intestine and made (primitive) line drawings of what he identified as meronts and micro- and macrogametocytes. He attributed various of these stages to large, medium, and small oocysts that he assigned to 3 different "new" species: *C. psammophi*, *C. hermae*, and *C. weyerae*, respectively. However, he never explained how he was able to distinguish endogenous stages of 1 *Caryospora* species from the other 2 when none of the endogenous stages he saw were known *a priori*. In other words, with 3 (?) species undergoing endogenous development at the same time, and in the same part of the intestine, how did he determine which stages went with which oocysts? Oocysts of these 3 species may be a continuum of sizes of a single species.

Norton and Pierce (1985) surveyed snakes for parasites from Balmoral, Zambia (15°33′S, 28°12′S) and found caryosporan oocysts in 1/1 *B. fuglinosus* and in 2/3 (67%) *P. sibilans*. Their sporulated oocysts all were similar in structure and also represented 3 distinct size classes (their Table 1, p. 61)—large, medium, and small—that they believed represented the 3 similar species identified and named by Bray (1960) as *C. psammophi*, *C. hermae*, and *C. weyerae*, respectively. Only *B. fuglinosus* had all 3 morphotypes in its feces, while both *P. sibilans* shed the large and medium-sized oocysts but not the small (= *C. weyerae*?) ones. The largest oocysts of Norton and Pierce (1985) were L × W: 35.5 × 33.1 (32–38 × 28–38), and sporocysts were L × W: 20.4 × 15.2 (19–22 × 14–16) in *B. fuglinosus*; in *P. sibilans* #1, oocysts were L × W: 34.3 × 32.5 (29–37 × 26–37), and sporocysts were L × W: 20.4 × 14.8 (18–24 × 13–16); and in *P. sibilans* #2, oocysts were L × W: 32.4 × 30.2 (30–34 × 23–31), but sporocysts were not measured. Also note that both *C. maxima* (Modrý et al., 1999) and *C. najadae* (Matuschka, 1986a) have similarly large oocysts.

Finally, Norton and Pierce (1985) fed sporulated oocysts (532 days old) from *B. fuglinosus* and oocysts from *P. sibilans* #1 and *P. sibilans* #2 (357, 268 days old, respectively) to coccidia-free white mice; the mice were examined 14 and 33 DPI by touch smears made from their intestine, kidney, liver, lymph nodes, diaphragm, heart, tongue, leg muscle, and brain, but no developmental stages were seen.

Caryospora pseustesi **Lainson, Nascimento and Shaw, 1991**

Type host: Spilotes sulphureus sulphureus (Wagler, 1824) (syn. *Pseustes sulphureus sulphureus* Beebe, 1946), yellow-bellied hissing snake or Amazon puffing snake (Colubridae).

Other hosts: None to date.

Type locality: Brazil: Pará State, Serra dos Carajás (6°S, 50°18′W).

Sporulated oocyst: Spheroidal (40%) to subspheroidal (60%); number of walls: 2, ~1.7 thick; wall characteristics: outer, smooth, golden yellow: thicker inner layer with prominent striations; L × W (N = 50): 26.4 × 25.4 (25–27.5 × 24–27.5); L/W ratio: 1.0 (1.0–1.1); M, OR, PG: all absent.

Sporocyst and sporozoites: Broadly ellipsoidal; L × W (N = 50): 18.9 × 13.8 (17.5–20 × 12.5–15); L/W ratio: 1.4 (1.2–1.4); SB, SSB, SR: all present; SB: nipple- or stopper-like; SSB: conspicuous, about same width as SB (line drawing); SR: disbursed granules or globules amongst the disbursed SZs; SZ: 1–2 RBs in each.

Prevalence: Unknown.

Sporulation: Unknown.

Remarks: Lainson et al. (1991) looked at the feces of "a number of snakes from Amazonia Brazil" when they described this species, but they failed to record the number of snakes infected with *C. pseustesi*.

Caryospora regentensis **Daszak and Ball, 2001**

Type host: Dendroaspis angusticeps (Smith, 1849), green mamba (Elapidae) (see Daszak and Ball, 2001b).

Other hosts: Dendroaspis viridis (Hallowell, 1844), western green mamba (Elapidae). Šlapeta et al. (2003) found oocysts in the western green mamba that they believed were also those of *C. regentensis* with only slight size differences.

Type locality: Kenya; exact locality unknown.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, ~0.5 thick; wall characteristics: smooth, colorless; L × W (N = 20): 16.8 × 16.4 (16–18 × 15–17); L/W ratio: 1.0; M, OR: both absent; PG: 1, large, bilobed (line drawing), adjacent to inner surface of the oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W: 13.0 × 10.3 (10–14 × 9–11); L/W ratio: 1.3; SB: caplike; SSB: a globular, ellipsoidal body, about same width as SB; SR: 15–20 large globules compacted within the curvature of the SZ and filling the sporocyst completely; SZ: 1 posterior RB was usually visible.

Prevalence: Daszak and Ball (2001) discovered this species in the only specimen of the type host they examined. They noted that their fecal sample was collected 17 months after the snake was imported into the UK and that the snake previously was held at the National Museum of Kenya, in Nairobi. Similarly, Šlapeta et al. (2003) found oocysts in the only specimen of *D. viridis* they examined from Malindi (03°21′S, 40°01′S) on coastal Kenya.

Sporulation: Unknown.

Remarks: One line drawing (their Fig. 5, p. 3) and 1 very light photomicrograph (Fig. 2, p. 2) were presented by

Daszak and Ball (2001a); a second line drawing (Šlapeta et al., 2003, Fig. 9, p. 27) and 2 good photomicrographs (their Figs. 3, 4, p. 24) add validity to this species. The sporulated oocysts of this species resemble those of *C. micruri* from *Micrurus s. spixii* in Brazil (Lainson et al., 1991); although similar in most structures the SR of the 2 forms is distinctly different. In addition to SR differences, the geographic isolation and evolutionary distances between the host species strongly suggest they are distinct species.

***Caryospora relictae* Telford, 1997**

Type host: Tantilla relicta Telford, 1966, Florida crowned snake (Colubridae).

Other hosts: None to date.

Type locality: USA: Florida, Marion County, Ocala National Forest, 0.7 km S Mud Lake (81°51′W, 29°17′N).

Sporulated oocyst: Mostly spheroidal; number of walls: 2; wall characteristics: outer, relatively smooth, thinner than inner layer; L × W (N = 51): 18.5 × 17.6 (16–22 × 15–20); L/W ratio: 1.05 (1.1–1.2); M, OR: both absent; PG: distinct, L × W: 2–2.5 × 1–1.5, appears to be attached to inner surface of oocyst wall (line drawing).

Sporocyst and sporozoites: Ovoidal; L × W (N = 51): 14.8 × 11.4 (12–17 × 10–16); L/W ratio: 1.3 (1.1–1.5); SB, SSB, SR: all present; SB: described only as "conspicuous," clearly caplike, sticking above sporocyst (line drawing); SSB: flat, about same width as SB (line drawing); SR: formed by an aggregate of ~15 granules; SZ: L × W: 10–14 × 2–2.5, with an ovoidal N, 2–3 wide situated between 2 ovoidal RBs.

Prevalence: Telford (1997) found this species in 4/42 (10%) specimens of the type host he examined.

Sporulation: Exogenous. Oocysts were placed in 2% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$), presumably at room temperature. Samples were checked in 3–5 days, at which time sporulated oocysts were found.

Remarks: Oocysts of this species closely resemble those of *C. gracilis* from the flat-headed snake found in Texas and Arkansas by Upton, McAllister, et al. (1992), but its oocysts are smaller in both length and width by 5–6, on average, and its sporocysts are shorter than those of *C. gracilis*.

***Caryospora sargentae* McAllister, Hnida and Trauth, 2022**

Type host: Tantilla gracilis Baird and Girard, 1853, flathead snake (Colubridae).

Other hosts: None to date.

Type locality: USA: Oklahoma, McCurtain County, Hochatown (34°10′17.0286″N, 94°45′05.7414″W).

Sporulated oocyst: Spheroidal to mostly subspheroidal; number of walls: 2, 1.4 (1.0–1.7) thick; wall characteristics: outer is tan, moderately pitted, ~0.9 (0.7–1.1); inner is smooth, 0.5 (0.3–0.5) thick; L × W (N = 30): 20.7 × 19.2 (17–24 × 16–21); L/W ratio: 1.1 (1.0–1.2); M: absent; OR: may be absent but 9/30 (30%) sporulated oocysts observed had 1 to several small, irregular spheroidal masses of nonrefractile debris; PG: present, attached to inner surface of oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W (N = 30): 15.0 × 11.0 (13–16 × 9–13); L/W ratio: 1.4 (1.2–1.6); SB, SSB, SR: all present; SB: nipple-like (N = 10): 2.0 (1.5–2.5) wide × 0.9 (0.5–1.0) high, rounded; SSB (N = 10): 2.7 (2.0–3.0) wide × 1.4 (1.0–1.5) high; SR: large, disbursed, irregular mass of various-sized granules located between and often obscuring SZs; SZ: neither RBs nor N were visible.

Prevalence: Found in the only specimen of the type host examined.

Sporulation: Probably exogenous. All oocysts sporulated within 48–72 hours.

Remarks: This is the fifth caryosporan described to date from the snake genus *Tantilla*, the others being *C. choctawensis* and *C. gracillis* from *T. gracilis* (McAllister et al., 2012; Upton, McAllister, et al., 1992) and *C. relictae* and *C. tantillae* from *T. relicta* (Telford, 1997). McAllister et al. (2022) summarized the morphological and size differences between the 5 species (their Table 1, p. 312) to allow interested readers to distinguish between them. In accordance with regulations listed in article 8.5 of the amended 2012 version of the International Code of Zoological Nomenclature, Mcallister et al. (2022) submitted details of this species to ZooBank to obtain its registration number.

***Caryospora saudiarabiensis* (Modrý, Koudela, Al-Oran and Amr, 1999) Duszynski and Upton, 2009**

Synonym: Caryospora "maxima" Modrý, Koudela, Al-Oran, and Amr, 1999 of Alyousif, Al Anzi and Al Shawa, 2004.

Type host: Echis carinatus (Schneider, 1801), saw-scaled or African carpet viper (Viperidae).

Other hosts: Alyousif et al., (2004) reported this coccidium as *C. maxima*, a parasite documented in *Psammophis schokari*, a colubrid snake in Jordan. Although the structures of their sporulated oocysts are nearly identical morphologically, it seems to me unlikely the 2 are the same species.

Type locality: Saudi Arabia: southern region in the area of Gazan (Alyousif et al., 2004).

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, 1.9 (1.5–2.3) thick; wall characteristics: yellow-brown outer layer; L × W (N = 50): 42.8 × 41.2 (40–46 × 40–44); L/W ratio: 1.0 (1.0–1.1); M, OR: both absent; PG: sometimes present as a small spheroidal body.

Sporocyst and sporozoites: Broadly ellipsoidal; L × W (N = 50): 22.1 × 16.8 (21–23 × 15.5–17); L/W ratio: 1.3 (1.2–1.5); SB, SSB, SR: all present; SB: domelike,1.3 high ×

3.4 wide (1–1.5 × 3–4); SSB: 3.7 high × 4.5 wide (3.5–4 × 4–5); SR: many granules in a compact mass lying centrally between SZs; SZ: banana-shaped, each with prominent anterior and posterior RBs that are spheroidal to subspheroidal with a round N lying between the RBs.

Prevalence: Found in 3/26 (12%) specimens of the type host examined (Alyousif et al., 2004).

Sporulation: Exogenous. Oocysts sporulated in an undetermined length of time in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution at 23–27°C.

Remarks: Histological sections showed meronts, macro- and microgamonts, and unsporulated oocysts to reside within epithelial cells of the small intestine. Alyousif et al. (2004) reported this coccidium as *C. maxima*, first described from *Psammophis schokari* by Modrý et al. (1999). Although nearly indistinguishable morphologically, except for the presence of a PG, no experimental evidence exists to support the conclusion that this colubrid caryosporan is capable of infecting a viperid host. Thus, it seems plausible that this coccidium represents a morphologically similar but different species, so Duszynski and Upton (2010) named it a new species, a decision with which I am still in agreement.

Caryospora serpentis **Upton, Freed, Burdick and McAllister, 1990**

Type host: Leioheterodon madagascariensis Duméril and Bibron, 1854, Madagascar hognose snake (Colubridae).

Other hosts: Madagascarophis colubrinus (Schlegel, 1837), Madagascar cat-eye snake (Pseudoxyrhophiidae); *Mimophis mahfalensis* (Grandidier, 1867), Malagasy colubrid (Colubridae).

Type locality: Madagascar.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, 1.2–1.6 thick; wall characteristics: outer, lightly pitted, ~0.8–1.2, inner is smooth, ~0.4 thick; L × W (N = 25): 17.1 × 17.0 (14–20 × 14–20); L/W ratio: 1.0 (1.0–1.1); M, OR: both absent; PG: 1 present, 2.2 wide, appears to be attached to inner surface of oocyst wall (line drawing).

Sporocyst and sporozoites: Ellipsoidal to ovoidal; L × W (N = 25): 13.8 × 10.2 (12–16 × 9–11); L/W ratio: 1.4; SB, SSB, SR: all present; SB: 1.3 high × 2.6 wide (1–2 × 2–3); SSB: 1.5 high × 3.1 wide (1–2 × 3–4); SR: numerous granules scattered among SZs; SZ: elongate vermiform, L × W: 12.0 × 3.0 (10–14 × 2.6–3.4); each with prominent anterior transverse striations and 2 RBs.

Prevalence: Found in 1/2 (50%) of the type host examined, in 2/6 (33%) *Mim. mahfalensis*, and in 3/4 (75%) of *Mad. colubrinus* from Madagascar.

Sporulation: Unknown; oocysts sporulated in the field before they reached the lab to be examined.

Remarks: Line drawing and 2 photomicrographs were included to support the original description. Upton, Freed, et al. (1990) summarized the other 4 *Caryospora*-type sporulated oocysts known from snakes to be similar to oocysts of *C. serpentis* at the time. Upton, Freed, et al. (1990) mentioned that Matuschka (1984a) had described a caryosporan collected from a *Coluber viridiflavus* in Italy that purportedly had 3 distinct size categories that were collectively named *C. colubris*. They said that this form had oocysts that were most similar to the small form of *C. colubris*, although the sporocysts were smaller.

Caryospora simplex **Léger, 1911**

Synonym: Karyospora simplex Léger, 1904 (*lapsus*).

Type host: Vipera aspis (L., 1758), European asp or asp viper (Viperidae).

Other hosts: Daboia palestinae (Werner, 1938) (syn. *Vipera palestinae* Werner, 1938), Palestine viper (Viperidae); *Daboia russelii* (Shaw and Nodder, 1797) (syn. *Vipera russellii* Strauch, 1869), Russel's viper (Viperidae) (Upton, 1986); *Montivipera xanthina* (Gray, 1849) (syn. *Vipera xanthina* Gray, 1849), Ottoman or coastal viper (Viperidae) (Upton, Ernst, et al., 1983); *Vipera ammodytes* (L., 1758), nose-horned or sand viper (Viperidae); *Vipera berus* (L., 1758), adder or northern viper (Viperidae); *Vipera kaznakovi* Nikolsky, 1909, Caucasus viper (Viperidae).

Type locality: France: region near Dauphine.

Sporulated oocyst: Spheroidal; number of walls: 1 (per Léger,1904, 1911), but there are at least 2 wall layers, ~1.4 thick; wall characteristics: outer surface colorless, lightly pitted, while inner layer is thicker; L × W: 14.9 (13.5–16); L/W ratio: 1.0; M, OR: both absent; PG: 1–2 present, 2.4 × 2.0 (2–3 × 1–2), attached to the inner surface of the oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W: 11.6 × 8.9 (10–13 × 8–9.5); L/W ratio: 1.3; SB, SSB, SR: all present; SB: L × W: 0.9 high × 2.5 wide (0.7–1.4 × 2–3); SSB: L × W: 1.3 high × 2.6 wide (0.9–1.4 × 2.3–2.7); SR: numerous granules of various sizes scattered among SZs; SZ: elongate vermiform, L × W: 11.4 × 2.3 (10–13 × 2–3); each with a central, spheroidal RB, ~1.8 wide, and a posterior RB, ~1.6 wide; N is situated between RBs.

Prevalence: Léger (1904) captured 2 *V. aspis* in the area near Dauphine, but only 1 was infected with monosporocystic oocysts, for which he named the genus and the type species of his new genus, *C. simplex*. Wilber et al. (1995) found this species in 2/2 (100%) *V. kaznakovi* in New Mexico, USA (snakes imported, but their captive history is unknown). Modrý et al. (1997) reported finding *C. simplex* oocysts in the feces of 9/17 (53%) *V. ammodytes* from Albania (0/1), Croatia (0/1), and Bulgaria (9/15), and in 32/37 (86%) *V. berus* from the Czech Republic (12/15), Slovak Republic (2/2), and England (18/20).

Sporulation: Exogenous. Sporulation occurred within 7 days at 27–30°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution (Upton et al., 1986).

Remarks: This is the **type species** of the genus *Caryospora*. Léger (1904) published a short, 2 paragraph note (an abstract?), in which he mentioned finding 2 different coccidian oocysts in the intestine of *V. aspis*; 1 was a typical *Isospora* sp. (= *Diplospora*) and the other an unusual form with 1 sporocyst containing 8 SZ. Referring to this newly discovered oocyst, "He gives this Coccidia, which becomes the type of a new family, the name *Karyospora simplex* n. sp." (p. 268). Unfortunately, neither the defining characters of this new family, nor measurements, line drawing(s), or photomicrographs of the stated new species accompanied Léger's (1904) brief note. Thus, his new undefined family and its new type species name became either *nomen dubium* (a name of unknown or doubtful application) or *nomen nudum* (a name that, if published before 1931, fails to conform to Article 12 of the International Code) at worst or a *species inquirendae* (a species of doubtful identity) at best.

Léger (1911) finally published a more reasonable but incomplete description of the oocyst and included some endogenous life cycle stages from tissue sections of the parasite in the intestine of 1 *V. aspis*; in that paper, he changed the spelling of the genus name to *Caryospora*, without explanation, and did not again mention *Karyospora*. Modrý et al. (1997) stated that the spelling in the 1904 paper was "a printer's error," (p. 99) but did not support that contention. Reichenow (1919) dated Léger's naming this genus to 1911 when, in fact, Léger first provided evidence for its existence, and technically he is correct. However, according to Article 23(b) of the International Code of Zoological Nomenclature, London, 1961, the senior synonym *Karyospora* should now be regarded as a *nomen oblitum* (forgotten name), since the spelling *Caryospora* had been adopted for more than 50 years. Also see Article 23.9.1.2 of the updated Code (Ride et al., 1999) that expands and supports this rule: "prevailing usage must be maintained when … the junior synonym … has been used for a particular taxon, as its presumed valid name, in at least 25 works published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years" (p. 28).

Léger's (1911) original description of *C. simplex*—although accompanied by 8 figures (plates) of 16 line drawings—is sketchy and incomplete by current-day standards. For example, he described the oocyst wall as ". . . well developed yellowish . . . on which there is a lenticular elevation that suggests the presence of a micropyle" (Léger, 1911, p. 77). Later work by Upton, Current, et al. (1983); Upton et al. (1986); and Modrý et al. (1997) demonstrated the presence of 1–2 PGs attached to the inner surface of the oocyst wall. Many details of oocyst, sporocyst and SZ structures and sizes, and details of the *in vivo* and *in vitro* developmental stages of *C. simplex* come from later authors (Galli-Valerio, 1929; Lavier, 1939; Upton, Current, et al., 1983; Upton, Ernst, et al., 1983; Upton, Current, Barnard, et al., 1984; Upton, Current, Ernst, et al., 1984; Upton, Haynes, et al., 1984).

A few of the early details of Léger's (1911) pioneering work on documenting the first species of *Caryospora* included spheroidal meronts, 8–10 long, that each produce 15–20 merozoites; ovoidal microgametocytes, 6–9 long, producing microgametes, 3 long, similar to other members of the Eimeriidae; spheroidal macrogamonts, 12–15 long; ovoidal monosporocysts, 12 × 8, with 8 SZ; endogenous stages developing supranuclear in intestinal epithelial cells of the posterior half of the middle segment of the snake small intestine; and his very interesting observation regarding sporogony, when the 8 SZs form directly within the oocyst without the formation of a sporocyst. Lavier (1939) also reviewed endogenous development of *C. simplex* in *V. aspis*.

Upton, Current, et al. (1983) redescribed the oocysts of *C. simplex* from the Ottoman viper, *M.* (= *Vipera*) *xanthina*, and their measurements are used above; they also did early experiments to show that *C. simplex*, like *C. bigenetica*, forms oocysts and caryocysts in the tongue and cheek of laboratory mice within 40 days after mice were inoculated orally with *C. simplex* oocysts. A year later, Upton, Current, Barnard, et al. (1984) described factors influencing the *in vitro* excystation of *C. simplex* at 25° and 37°C and the motility and structure of excysted SZs. Once clean SZ could be isolated from oocysts/sporocysts, Upton, Haynes, et al. (1984) inoculated monolayers of human embryonic lung cells with 30,000 or 70,000 SZ of *C. simplex* and watched their progression from penetrating lung cells (2–6 DPI), developing into Type I meronts containing 8–22 short merozoites (6–16 DPI) and then Type II meronts producing 8–22 long, slender merozoites (10–18 DPI) that penetrated other cells, producing undifferentiated gamonts (14–16 DPI), to observing mature micro- and macrogametes and thin-walled unsporulated oocysts (16–18 DPI), but they were unable to get these oocysts to sporulate, and Swiss-Webster mice injected intraperitoneally with merozoites on 10 DPI did not become infected. Their study (Upton, Haynes, et al., 1984) was only the second time a coccidian species was documented to develop from SZ to oocysts in cell culture.

Upton et al. (1985) studied mouse-to-mouse (*Mus musculus*) transmission of *C. simplex* to determine if the monozoic caryocysts (of Wacha and Christiansen, 1982) were

infective to mice to determine if cannibalism may play a role in the transmission and maintenance of this parasite in rodent communities. Mice (Group A) inoculated with 250,000 sporulated oocysts from the Ottoman viper, *M. xanthina*, had developmental stages of *C. simplex* on 10, 15, 18, and 25 DPI. Mice in Group B, inoculated with infected cheek dermis from Group A mice had numerous caryocysts in their cheek dermis at 25 DPI, and mice in Group C that received infected tissues from Group B mice had markedly larger numbers of caryocysts in their cheek dermis than did mice in either Group A or B. Their study demonstrated that *C. simplex* can be transferred via caryocysts between mice and that the caryocysts produced are identical to oocyst-induced infections, suggesting to Upton et al. (1985) that in nature, *C. simplex* may be propagated in mouse populations via cannibalism without the need for snake-derived oocysts.

Upton and Barnard (1986) used 4 lab-reared, Palestine viper (*D. xanthina palestinae*) littermates to determine transmission modes of *C. simplex* in snakes. One snake (#149) was inoculated *per os* with 5×10^4 sporulated oocysts obtained from the feces of an Ottoman viper (*M. xanthina*); it began passing unsporulated oocysts of *C. simplex* 121 DPI. A second littermate (#150) was fed 5 mice that had been inoculated orally 25 days previously with 5×10^4 sporulated oocysts of *C. simplex*; it began passing unsporulated oocysts of *C. simplex* 33 days after eating the first 2 of 5 infected mice. The third littermate (#151) was inoculated *per os* with sporulated oocysts from viper #150 and began passing unsporulated oocysts 52 DPI. The final littermate (#152) was the uninfected control and did not pass oocysts. This study demonstrated that snake/snake and mouse/snake transmission of *C. simplex* readily occurs in nature.

Finally, Wilber et al. (1995) identified *C. simplex* oocysts from the feces of 2 captive female Kaznakov's vipers in a zoo in Albuquerque, New Mexico, and detected its meronts and gamonts in the intestinal epithelial cells of another female Kaznakov's viper that died in captivity. A year later, in a survey of 2 *Vipera* species in Europe, Modrý et al. (1997) reported *C. simplex* oocysts in the feces of *V. ammodytes* and *V. berus* from several European countries. They also inoculated 8–11-week-old SCID mice *per os* with a combination of 4 isolates from *V. berus* and 3 *Caryospora* isolates from *V. ammodytes*. All inoculated mice exhibited lethargy, rough hair coat, and considerable swelling of the facial tissue, foot pads, and scrota (males) or external genitalia (females) from 8 DPI. After 8 DPI, more pronounced clinical signs were evident, and no SCID mice survived > 28 DPI. Histological exams showed extensive areas of inflammatory edema in skin, subcutis, and adjacent muscular tissue, mainly in nose and facial tissue at the base of ears, footpads, scrotum (males) or external genitalia (females), and endogenous stages (meronts, gamonts, oocysts, caryocysts) were abundant and morphologically identical with those described by Upton, Current, Barnard, et al. (1984).

***Caryospora tantillae* Telford, 1997**

Type host: Tantilla relicta Telford, 1966, Florida crowned snake (Colubridae).

Other hosts: None to date.

Type locality: USA: Florida, Marion County, Ocala National Forest, 5 km W Lake Delancy (81°49'W, 29°24'N).

Sporulated oocyst: Mostly spheroidal; number of walls: 2 ("bilaminate"), but Telford's (1997) line drawing (his Fig. 20, p. 21) shows at least 4 layers; wall characteristics: not mentioned; L × W (N = 59): 19.6 × 18.9 (16–22 × 16–21); L/W ratio: 1.0 (1.0–1.1)); M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal; L × W (N = 59): 15.1 × 11.6 (12–17 × 10–13); L/W ratio: 1.3 (1.1–1.6); SB, SR: both present; SSB: absent; SB: described only as "prominent," clearly caplike, sticking above sporocyst (line drawing); SR: ~6.0 wide, appearing as an aggregation of granules; SZ: 14 × 2.5, with a N, 2–3 wide, between 2 ovoidal RBs.

Prevalence: Telford (1997) found this species in 6/42 (14%) specimens of the type hosts he examined.

Sporulation: Exogenous. Oocysts were placed in 2% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$), presumably at room temperature. Samples were checked in 3–5 days, at which time sporulated oocysts were found.

Remarks: Oocysts of this species somewhat resemble those of *C. gracilis* from the flat-headed snake found in Texas and Arkansas by Upton, McAllister, et al. (1992), but its oocysts are smaller by 4–5, on average, in both length and width, and it lacks a PG. Also, its sporocysts are shorter and lack a SSB, which those of *C. gracilis* possess.

***Caryospora telescopis* Matuschka, 1986b**

Type host: Telescopus fallax (Fleischmann, 1831), European or Mediterranean cat snake (Colubridae).

Other hosts: None to date.

Type locality: Greece.

Sporulated oocyst: Spheroidal; number of walls: 2, ~1.0 thick; wall characteristics: smooth; L × W (N = 10): 21.5 (19–23.5); L/W ratio: 1.0; M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal; L × W: 15.0 × 11.4 (15–16 × 11–12); L/W ratio: 1.3; SB, SSB, SR: all present; SB: nipple-like, sticking above sporocyst (line drawing); SSB: flat, about same width as SB; SR: a cluster of spheroidal bodies scattered among SZ; SZ: not mentioned or measured by Matuschka (1986b).

Prevalence: Found in the only cat snake examined by Matuschka (1986b).

Sporulation: Exogenous. Oocysts became fully sporulated in about 48 hours after feces were placed into 2.5% potassium dichromate ($K_2Cr_2O_7$) solution at 21–25°C.

Remarks: Matuschka (1986b) compared the oocyst and sporocyst sizes of *C. teloscopis* to those of the 18 other caryosporan species known from ophidian hosts in 1986 (his Table 1, p. 96) and said his oocysts resembled those of 6 caryosporan species from 6 different hosts (1 boid, 4 colubrids, 1 elaphid). In particular, he said his oocysts most resembled those of *C. bengalensis* from the freshwater snake *Enhydris enhydris*, *C. hermae* from *Psammophis phillipsi*, *C. brasiliensis* from *Phylodryus aestivus*, *C. lampropeltis* from *Lampropeltis calligaster*, *C. coralle* from *Corallus caninus* (boid), and *C. demansiae* from *Dermansia psammophis* (elaphid). The exact details of the differences between these 7 caryosporans is discussed by Duszynski and Upton (2009, p. 82) for those interested in such details.

***Caryospora veselyi* Modrý and Koudela, 1998**

Type host: Ahaetulla nasuta (Lacépède 1789), long-nosed tree or whip snake (Colubridae).

Other hosts: None to date.

Type locality: India: Tamilnadu, 10 km N of Mammalapuram, 40 km N of Madras.

Sporulated oocyst: Spheroidal; number of walls: 2, ~1.5 thick; wall characteristics: outer layer slightly pitted, 2/3rds of total thickness; L × W: 18.9 (16.5–21.5); L/W ratio: 1.0; M: absent; OR: in about 30% of the oocysts a group of small granules, each < 0.5 wide, were seen representing an indistinct OR; PG: an irregular granule, ~2.0 × 1.0, was observed attached to the inner oocyst wall in 35% of the sporulated oocysts.

Sporocyst and sporozoites: Ovoidal to ellipsoidal; L × W: 13.7 × 10.3 (13–15.5 × 9–11); L/W ratio: 1.3 (1.2–1.4); SB, SSB, SR: all present; SB: knoblike, 1.0 high × 2.0–3.0 wide; SSB: a homogeneous globule, 1.0–1.5 high × 2.5–4.5 wide; SR: small granules of irregular size scattered between SZs; SZ: lie around the SR and each with both an anterior and a posterior RB and a visible N that lies between RBs.

Prevalence: Found in 1/4 (25%) specimens of the type host examined.

Sporulation: Exogenous. Oocysts became fully sporulated in 3 days when maintained in 2.5% aqueous potassium dichromate ($K_2Cr_2O_7$) solution held at 20–23°C.

Remarks: Modrý and Koudela (1998) also found oocysts of *C. ahaetullae* (Modrý and Koudella, 1994) in the same snake infected with *C. veselyi*. Sporulated oocysts of this species are easily distinguished from those of *C. ahaetullae* by their significantly smaller oocyst and sporocyst dimensions and the SB and SSB structures, among others.

***Caryospora weyerae* Bray, 1960**

Type host: Psammophis phillipsii Hallowell, 1844 (syn. *P. sibilans phillipsi* Loveridge, 1840), hissing, olive, or western sand snake (Psammophiidae).

Other hosts: None.

Type locality: Liberia, presumably near Harbel.

Sporulated oocyst: Subspheroidal; number of walls: 2; wall characteristics: thin, colorless, smooth layers; L × W: 16.1 × 14.9 (14–18 × 13–17); L/W ratio: 1.1; M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal (line drawing); L × W: 13.3 × 10.0 (12–14 × 9–11); L/W ratio: 1.3; SB: present (line drawing); SSB: may or may not be present as it is not mentioned in the description nor is one included in the line drawing; SR: a few small, scattered granules; SZ: not described.

Prevalence: Bray (1960) examined 4 adult and 1 juvenile sand snakes and only the juvenile (1/5, 20%) was passing oocysts of 3 caryosporan species, all of which he described as new.

Sporulation: Unknown.

Remarks: Bray (1960) fixed a piece of tissue of the intestine of the juvenile snake that was passing oocysts and said, "the coccidia were traced up the intestine and a piece of intestine at the point of the cessation of oocyst production was excised . . . and fixed." He then studied stained tissue sections of that piece of intestine and made (very primitive) line drawings of what he identified as meronts and micro- and macrogametocytes. He attributed various of these stages to large, medium, and small oocysts that he assigned to 3 different "new" species, *C. psammophi, C. hermae,* and *C. weyerae,* respectively. However, he never explained how he was able to distinguish endogenous stages of 1 *Caryospora* species from the other 2 when none of the endogenous stages he saw were known *a priori*. In other words, with 3 (?) species undergoing endogenous development at the same time, and in the same part of the intestine, how did he determine which stages went with which oocysts? Oocysts of these 3 species may be a continuum of sizes of a single species.

Norton and Pierce (1985) surveyed snakes for parasites from Balmoral, Zambia (15°33′S, 28°12′S) and found caryosporan oocysts in 1/1 *B. fuglinosus* that represented 3 distinct size classes (their Table 1, p. 61), large, medium, and small; they believed their smallest oocysts were nearly identical to those described earlier by Bray (1960) as *C. weyerae*. These smallest oocysts of Norton and Pierce (1985) were L × W: 14.3 × 14.1 (14–15 × 13–15) with sporocysts that were, L × W: 12.8 × 9.5 (11–14 × 9–10).

Finally, Norton and Pierce (1985) fed sporulated oocysts (532 days old) from *B. fuglinosus* to coccidia-free white

mice; the mice were examined 14 and 33 DPI by touch smears made from their intestine, kidney, liver, lymph nodes, diaphragm, heart, tongue, leg muscle, and brain but no developmental stages were found in any of these tissues.

***Caryospora zacapensis* Seville, Asmundsson and Campbell, 2005**

Type host: Masticophis mentovarius (Duméril, Bibron and Duméril, 1854), neotropical whip snake (Colubridae).

Other hosts: None.

Type locality: Guatemala: Zacapa, San Vicente, Area El Arenal (14°10.05'N, 90°58.01'W).

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, 1.7 thick; wall characteristics: outer, yellow-brown, lightly pitted, 1/2–3/4 of total thickness; L × W (N = 48): 22.5 × 21.8 (19–25 × 18–25); L/W ratio: 1.0; M, OR: both absent; PG: 1, large, refractile, adjacent to inner surface of the oocyst wall.

Sporocyst and sporozoites: Ovoidal; L × W: 14.6 × 11.4 (11–16 × 10–13); L/W ratio: 1.3; SB: large, nipple-like; SSB: large globular body, wider than SB; SR: a central mass and a few disbursed small granules; SZ: sausage-shaped, curled around granules of SR; RB, N: not observed or mentioned.

Prevalence: Seville et al. (2005) discovered this species in 2/2 (100%) specimens of the type host they examined.

Sporulation: Unknown. Oocysts sporulated in the field.

Remarks: One line drawing and 3 photomicrographs presented to support the new species description. Only 1 other caryosporan is known from *Masticophis*: *C. masticophis* described from *M. flagellum* collected in Arkansas (USA) by Upton et al. (1994), but the oocysts and sporocysts of *C. zacapensis* are distinctly larger than those of *C. masticophis* along with other structural differences pointed out by Seville et al. (2005).

Caryospora *species in turtles (1)*

***Caryospora cheloniae* Leibovitz, Rebell and Boucher, 1978**

Synonym: Caryospora sp. of Robell, 1974.

Type host: Chelonia mydas mydas (L., 1758), green turtle (Cheloniidae).

Other hosts: None to date.

Type locality: British West Indies: Grand Cayman.

Sporulated oocyst: Elongate ellipsoidal with long axis curved to varying degrees, like a cucumber or sausage; number of walls: 2, thin, ~0.5 (0.3–0.6); wall characteristics: smooth, fragile, irregular, and during sporulation it often disintegrates, releasing its sporocyst such that only 6/1,000 sporulated sporocysts were found within the oocyst wall (Leibovitz et al., 1978); L × W: 37.4 × 12.8 (34–40 × 11–15); L/W ratio: 2.9; M, OR, PG: all absent.

Sporocyst and sporozoites: Elongate cylindroidal with long axis curved to varying degrees like the oocyst; L × W: 34.5 × 12.7 (26–44 × 11–17); L/W ratio: 2.8 (1.5–4.2); SB: distinct, as a thin, elevated dome, L × W: 2.0 high × 4.6 wide (1–3.5 × 2–6); SSB: a colorless lenticular body under the SB, L × W: 1.3 high × 3.8 wide (1–2 × 2–6); PSB: absent, but at end of sporocyst opposite SB/SSB is a fine, median fissure that traverses the sporocyst wall from its internal to its external surface, and ends of the fissure are elevated as tiny knoblike projections; SR: a spheroidal mass, L × W: 11.4 × 9.7 (7–19 × 7–12), composed of coarse granules at its surface with less dense, finer granules internally, centrally located in sporocyst with SZ extending toward the poles of sporocyst; SZ: club or cigar-shaped, L × W (N = 25): 13.3 × 2.8 (13–17 × 2–4), with 1 rounded end and the other end pointed; both anterior and posterior RBs present with a small, round N between them.

Prevalence: Leibovitz et al. (1978) collected oocysts from feces and necrotic intestinal tissue from stock hatchlings and juvenile tank-reared green sea turtles. Gordon et al. (1993a, b) found it in 26/26 (100%) selected from 70 wild green turtles over a 6-week period in the spring of 1991 and again in 3 more turtles over October–December 1992.

Sporulation: Exogenous. A few oocysts (< 1%) completely sporulated in 19.5 hours at 25°C when placed into 2.5% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution, but even after 98 hours, only 92/672 (14%) had sporulated (Leibovitz et al., 1978). Gordon et al. (1993a, b) put oocysts in filtered sea water for 5 days at 28°C but said sporulation was completed in 15–24 hours. However, within 24 hours the sporocysts split transversely into 2 unequal parts and all SZs exited the sporocyst and arranged themselves into a starlike pattern, attached by their obtuse ends, to resemble a radiolarian. These starlike structures remained intact for 2 to 3 days, after which they disintegrated (Gordon et al., 1993b).

Remarks: Rebell et al. (1974) first identified this caryosporan when they reported an epidemic of coccidian disease in 2 groups of recently hatched green turtles in the spring of 1973, but they did not name it. The disease, and its associated mortality, appeared in young turtles about 30 days after hatching and ran a 60-day course through the stock hatchlings. The turtles were raised in a series of fiberglass tanks at Mariculture, Ltd., Grand Caymen, British West Indies. In addition to being the first *Caryospora* reported from turtles, the life cycle is distinctive because of its division by transverse binary fission and the structure of the sporulated oocysts. *Caryospora cheloniae* produces marked tissue destruction in the hindgut; is the first, and

still only, serious coccidian pathogen reported from turtles; and is an economically important pathogen of mariculture-reared green sea turtles (Leibovitz, et al., 1978). Rebell et al. (1974) noted that the epidemic caused by this parasite was unprecedented in the history of the Mariculture Ltd. farm and that the coccidium may have been introduced in sand brought from Ascension Island or from Surinam. It also is possible the parasite naturally infected turtles at the farm but remained undetected until management circumstances permitted it to reach epidemic proportions. It is likely that once more turtles became infected and large numbers of oocysts were constantly being released into the well-aerated water, a condition that favored sporulation was created and the epidemic that resulted.

Gordon et al. (1993b) found something not reported in the original description of the oocyst and sporocyst by Leibovitz et al. (1978); they (1993b) said that no sporocysts were observed within oocysts, and the sporocysts they measured (N = 19) were larger than those in the original description, L × W: 44 × 13 (37–51 × 10–16), although the ranges did overlap. The other difference between the 2 reports of infection in the British West Indes (Leibovitz et al., 1978) and that reported from Australia (Gordon et al., 1993a, b) is that the former occurred only in juvenile turtles during cultivation in laboratory tanks, while the latter was found only in free-living adults. Development in extraintestinal sites is not unprecedented in some coccidia (e.g., Novilla et al., 1981) and may be relatively common in poikilotherms (Overstreet, 1981). In fact, a number of studies have demonstrated facultatively heteroxenous life cycles of other *Caryospora* species involving secondary hosts in which extraintestinal development occurs (Lindsay and Sundermann, 1989; Dubey et al., 1990; Douglas et al., 1991; Douglas, Sundermann and Lindsay, 1992; Douglas, Sundermann, Lindsay and Mulvaney, 1992).

Caryospora Species Inquirendae—*Birds (5)*

***Caryospora* sp. of Liu, Brice, Elliot, Ryan and Yang, 2019**

Original host: Grallina cyanoleuca (Latham, 1801), magpie lark (Monarchidae).

Remarks: Liu et al. (2020) found this *Caryospora*-like isolate in a single magpie lark collected in Western Australia. Sporulated oocysts were subspheroidal and measured L × W (N = 35): 21.5 × 19.0 (20–24 × 18–20); L/W ratio: 1.1; M, OR, PG: all absent. Ellipsoidal sporocysts were L × W (N = 35): 18.9 × 12.3 (17–21 × 12–13); L/W ratio: 1.5; SB: present, small, flattened; SSB: trapezoidal, slightly wider than SB (line drawing); SR: present as small granules scattered throughout the sporocyst; SZ: vermiform, with anterior striations and both anterior and posterior RBs, however the authors (*lapsus calami*) mistakenly gave exactly the same measurements for the SZ as they had presented for the sporocyst, twice, both in their abstract and their results sections. Molecular characterization of this Australian isolate was conducted at the 18S rRNA and the mitochondrial cytochrome oxidase (COI) loci; at the 18S rRNA locus their isolate exhibited 88.8% to 96.5% similarity with other *Caryospora* species from different hosts. At the COI locus, it showed 91.5% similarity to *Caryospora* cf. *bigenetica* from a rattlesnake, *Sistrurus catenatus* (Rafinesque, 1818), eastern massasauga. No attempt to further identify this morphotype was made, but the authors provided a useful table (Table 1), comparing the hosts and structural features of their morphotype with other *Caryospora* species. Unfortunately this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

***Caryospora* sp. of Varghese and Yayabu, 1981**

Original host: Diphyllodes magnificus (Pennant, 1781), magnificent bird-of-paradise (Paradisaeidae).

Remarks: Varghese and Yayabu (1981) reported on a survey of coccidia and helminth parasites in fecal samples of 218 birds belonging to 24 families in 13 avian orders. They (1981) made provisional and very superficial identifications of 5 types of oocysts and eggs recovered from the fecal matter of each of 2 magnificent birds-of-paradise, including 1 form of *Caryospora*-like oocysts. They took no measurements and based their identification on oocysts with 1 sporocyst containing 8 SZ. Confirming their decision they said, "We have observed over a hundred oocysts in the fecal matter from each of the 2 magnificent bird-of-paradise (*D. magnificus*) specimens, and these are provisionally identified as belonging to the genus *Caryospora*" (Plate 1) (p. 105). They gave no measurements, but their figure 4 (line drawing, p. 106) showed an oocyst lacking M and OR but with a single PG that seemed to be attached to the inner oocyst wall; the sporocyst had a prominent, nipple-like SB but lacked SSB and PSB, and SZs were not clearly distinguishable one from the other, although globules were drawn that might represent a disbursed SR.

***Caryospora* sp. of Wetzel and Enigk, 1939**

Synonym: Non *Caryospora falconis* Wetzel and Enigk (1939).
Original host: Athene noctua (Scopoli,1769), little owl (Strigidae).

Remarks: No figures or descriptions given. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

***Caryospora* sp. of Yakimoff and Matschulsky, 1936 (ovoidal form)**

Synonym: Caryospora henryi, ovoidal/ellipsoidal form, in part, of Yakimoff and Matschoulsky (1936).

Original host: Milvus migrans (Boddaert,1783), black kite (Accipitridae).

Remarks: Yakimoff and Matschulsky (1936) reported 2 distinct morphotypes of caryosporan oocysts from *M. migrans*. The ellipsoidal forms were L × W: 36.8 × 28.1 (31–45 × 27–36); L/W ratio: 1.3. Böer (1982) interpreted their (1936) oblong oocysts as *C. kutzeri* and this also was suggested by Upton, Campbell, et al. (1990). No figures or descriptions given. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

***Caryospora* sp. of Yakimoff and Matschulsky, 1936 (round form)**

Synonym: Caryospora henryae, round form, in part, of Yakimoff and Matschulsky (1936).

Original host: Milvus migrans (Boddaert,1783), black kite (Accipitridae).

Remarks: Yakimoff and Matschulsky (1936) reported 2 distinct morphotypes of caryosporan oocysts from *M. migrans*. The spheroidal forms were 35.3 wide (31–36); L/W ratio: 1.0. Böer (1982) interpreted the spheroidal oocysts they (1936) found as end views of *C. henryae*. Upton, Campbell, et al. (1990) suggested that the spheroidal oocysts of Yakimoff and Matschulsky (1936) likely were those of *C. falconis*. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

Caryospora Species Inquirendae—*Lizards (2)*

***Caryospora* sp. 4 of Koudela, Modrý, Volf and Šlapeta, 2000**

Original host: Varanus niloticus (L., 1766), Nile monitor (Varanidae).

Remarks: No images of sporulated oocysts were given except for 1 photomicrograph of a macrophage with 2 oocysts within it, but sporocysts were on end view. Oocysts were collected from the feces of 1 *V. niloticus*, but no figures or descriptive parameters were given. This was 1 of the caryosporans from different hosts and localities tested in SCID mice to elucidate if they had a heteroxenous life cycle pattern. This morphotype did not exhibit a heteroxenous pattern. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

***Caryospora varani* of Kaur and Oberoi, 1987**

Original host: Varanus sp. Merrem, 1820, carnivorous lizard (Varanidae).

Remarks: No qualitative or quantitative descriptive parameters were given or pictured, although a plate that is unreadable says that a sporocyst, microgametocyte, and macrogametocyte are pictured (Kaur and Oberi, 1987). Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

Caryospora Species Inquirendae—*Mammals (1)*

***Caryospora* spp. in dogs of Macrone, 1908 and others**

Original host: Canis familiaris L. 1758, domestic dog (Canidae).

Remarks: Dermal coccidiosis, with *Caryospora*-like organisms, has been reported in dogs in Italy (Marcone, 1908) and the United States (Shelton et al., 1968; Sangster et al., 1985; Sundermann, Blagburn, et al., 1988; Lindsay and Sundermann, 1989; Dubey et al., 1990). The parasite reported by Marcone (1908) cannot be determined because of its inadequate description and the lack of illustrations (Dubey and Speer, 1991). The parasite reported by Shelton et al. (1968) is probably the same *Carayospora* sp. reported by Dubey et al. (1990), and the parasite reported by Sangster et al. (1985) was shown retrospectively to be the same *Caryospora* sp. of Dubey et al. (1990).

Infected dogs have nodules in their skin, and these nodules often have serohaemorrhagic exudate. Anorexia, lethargy, and ocular and nasal discharge usually present with this infection, and a concomitant canine distemper was associated with 2 of the dogs examined. Sangster et al. (1985) suggested that there is a relationship between immunosuppression and the development of dermal coccidiosis due to this *Caryospora* species in dogs. Lindsay and Sundermann (1989) reported that the epidermis covering these nodules usually is thickened except in areas of ulceration, and the fibrinocellular exudate may be present. The dermis is edematous and infiltrated with macrophages, plasma cells, and polymorphonuclear cells. Eosinophils are also abundant in infected areas, resulting in inflammation that may extend to the subcutis and subcutaneous muscles. *Caryospora* sp. meronts and gamonts are usually small, and they occur in connective tissue cells (Lindsay and Sundermann, 1989).

Dubey et al. (1990) found 2 2-month-old bulldogs in Georgia infected with a *Caryospora* sp. Numerous developmental stages were seen in the skin and lymph nodes with severe pyogranulomatous dermatitis. Meronts were ~20

long with up to 25 merozoites. Gamonts, unsporulated and sporulated oocysts, and caryocysts were found in macrophages, connective tissue cells, and in other host cells. Caryocysts were up to 18 long, each with 1–3 sporozoites. Dubey et al. (1990) said that all developmental stages of this *Caryospora* sp. reacted positively with anti–*Caryospora bigenetica* serum examined in an immunoperoxidase test. This caryosporan has not yet been assigned a binomial to distinguish it from others.

Caryospora Species Inquirendae—*Snakes (16)*

***Caryospora* sp. of Daszak, 1995**

Original host: Casarea dussumieri (Schlegel, 1837), Round Island boa (Bolyeriidae).

Remarks: Daszak (1995) published an overview of the prevalence of endoparasites in Round Island reptiles. The study was hindered by the fact that only feces could be collected, since reptiles on the island are protected. He only mentioned that 6/10 (60%) samples from *C. dussumieri* had oocysts of a *Caryospora,* "that has a fairly uniform morphology and size range between samples," indicating that likely only 1 *Caryospora* species was present. No other information was provided. It would be interesting to learn more about this morphotype and all island-bound apicomplexans.

***Caryospora* sp. of Fernandes–Grego, Gardiner and Catão–Dias, 2004**

Original host: Bothrops jararaca Weid, 1824, jaracara (Viperidae).

Remarks: Frenandes-Grego et al. (2004) studied the comparative pathology of parasitic infections in free-ranging and captive pit vipers. They mentioned seeing stages of a *Caryospora* species in 1/45 (2%) jaracara intestines they examined microscopically. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

***Caryospora* sp. of Frye, 1981**

Original host: Python sp. (Pythonidae).

Remarks: Frye (1981) mentioned the presence of a caryosporan-like form in a python in his book on biochemical and surgical aspects of captive reptile husbandry. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

***Caryospora* sp. of Hoge–1 (*Bothrops* spp.), 1991**

Original hosts: Bothrops jararaca (Wied-Neuwied, 1824), jararaca; *Bothrops neuwiedi* Wagler, 1824, Neuwied's lancehead (Viperidae).

Remarks: Hoge's (1991) dissertation at the Universidade de São Paulo, Brazil, involved examining viperid and colubrid snakes of Brazil for coccidians, especially looking for stages of *Caryospora, Sarcocystis*, and *Eimeria* species. Her methods included looking only at the feces from some snakes and/or detailed examination of the intestinal tract of others, but it was not clear in her methods if the intestines examined were the same as or different from those from which she took feces. In addition, her results are difficult to comprehend because in some cases she stated the percentage of snakes of 1 species in which *Caryospora* oocysts were found, but she did not give the actual number of individual snakes examined. Her methods (p. 13) stated that feces from 56 snakes in the genera *Bothrops* (8 species) and *Crotalus* (3 subspecies) were examined for oocysts, but the numbers in her tables are not congruent with that statement. As best I could determine from her results, only 1/4 (25%) *B. jararaca* and 1/6 (17%) *B. neuwiedi* (her Tables 2, 3) had oocysts of an unknown *Caryospora* sp. in their feces. On the other hand, she stated, "The tests carried out showed the following results: in 49 snakes of the genus *Bothrops* sp. examined, 18.4% presented *Caryospora* sp." (Hoge, 1991, p. 19).

***Caryospora* sp. of Hoge–2 (*Crotalus* sp.), 1991**

Original host: Crotalus durissus L.,1758, Cascabel rattlesnake (Viperidae).

Remarks: Hoge's (1991) dissertation at the Universidade de São Paulo, Brazil, involved examining viperid and colubrid snakes of Brazil for coccidians, especially looking for stages of *Caryospora, Sarcocystis* and *Eimeria* species. Her methods included looking only at the feces from some snakes and/or detailed examination of the intestinal tract of others, but it was not clear in her methods if the intestines examined were the same as or different from those from which she took feces. In addition, her results are difficult to comprehend because in some cases she stated the percentage of snakes of 1 species in which *Caryospora* oocysts were found, but she did not give the actual number of individual snakes examined. Her methods (p. 13) stated that feces from 56 snakes in the genera *Bothrops* (8 species) and *Crotalus* (3 subspecies) were examined for oocysts, but the numbers in her tables are not congruent with that statement. As best can be determined from the results only 7/13 (54%) *C. durissus* had oocysts of an unknown *Caryospora* sp. in their feces.

***Caryospora* sp. of Hoge–3 (*Tomodon* sp.), 1991**

Original host: Tomodon dorsatus Duméril, Bibron et Duméril, 1854, Pampas snake (Colubridae).

Remarks: Hoge's (1991) methods included looking only at the feces from some snakes and/or detailed examination of the intestinal tract of others, but it was not clear in her methods if the intestines examined were the same as or different from those from which she took feces. In addition, her results are difficult to comprehend because in some cases she stated the percentage of snakes of 1 species in which *Caryospora* oocysts were found but did not give the actual number of individual snakes examined. For example, she stated, "On the other hand, 43% of the snakes of the species *T. dorsatus* presented parasitic forms of *Caryospora*" (Hoge, 1991, p. 19), but she didn't state the number of *T. dorsatus* samples examined.

***Caryospora* sp. 1 of Koudela, Modrý, Volf and Šlapeta, 2000**

Original host: Calloselasma rhodostoma (Kuhl, 1824), Malayan ground pit viper (Viperidae).

Remarks: Oocysts were found in the feces, but no figures or descriptive parameters were given. This was one of the caryosporans from different hosts and localities tested in SCID mice to elucidate if they had a heteroxenous life cycle pattern. This morphotype did exhibit a heteroxenous pattern.

***Caryospora* sp. 2 of Koudela, Modrý, Volf and Šlapeta, 2000**

Original host: Atheris nitschei Tornier, 1902, Nitsche's bush viper (Viperidae).

Remarks: Oocysts were found in the feces, but no figures or descriptive parameters were given. This was one of the caryosporans from different hosts and localities tested in SCID mice to elucidate if they had a heteroxenous life cycle pattern. This morphotype did exhibit a heteroxenous pattern.

***Caryospora* sp. 3 of Koudela, Modrý, Volf and Šlapeta, 2000**

Original host: Vipera ursinii (Bonaparte, 1835), Ursini's viper (Viperidae).

Remarks: Oocysts were found in the feces, but no figures or descriptive parameters were given. This was one of the caryosporans from different hosts and localities tested in SCID mice to elucidate if they had a heteroxenous life cycle pattern. This morphotype did exhibit a heteroxenous pattern.

***Caryospora* sp. of Matuschka, 1986b**

Original host: Vipera kaznakovi Nikolsky, 1909, Caucasus viper (Viperidae).

Remarks: Matuschka (1986b) reported caryosporan oocysts in the feces of 1 *V. kaznakovi* collected in western parts of the Caucasus in Turkey and presented 3 photomicrographs (Figs. 4–6, p. 95). Oocysts were excreted unsporulated. Sporulated oocysts were spheroidal, with a smooth, bilayered wall, ~1.0 thick, and measured, L × W (N = 40): 12.7 (11–14); L/W ratio: 1.0; M, OR: both absent; PG: present. Sporocysts were L × W: 11.7 × 8.0; L/W ratio: 1.5; SB, SSB: both present; SR: a cluster of several spheroidal bodies completely filling the sporocyst. He did not provide a binomial for reasons explained in detail in Duszynski and Upton (2009, p. 207). Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

***Caryospora* sp. 1 of Modrý, 1998**

Original host: Ateris nitschei Tornier, 1902, Niche's bush viper (Viperidae).

Remarks: Modrý (1998) experimentally inoculated SCID mice with a caryosporan from a Ugandan bush viper, and they became infected; however, he was unable to transmit the infection to *Viper ammodytes*, the long-nosed viper. This "species" was mentioned briefly in his PhD dissertation (Modrý, 1998) but never published because oocysts were impossible to distinguish from *C. simplex/C. bigenetica*.

***Caryospora* sp. 2 of Modrý, 1998**

Original host: Calloselasma rhodostoma Boie, 1827, Malayan pit viper (Viperidae).

Remarks: Modrý (1998) experimentally inoculated SCID mice with a caryosporan from a Malayan pit viper, and they became infected; however, he was unable to transmit the infection to *V. ammodytes*, the long-nosed viper; to *Crotalus atrox*, the western diamondback rattlesnake; or to *Gloydius blomhoffi*, mamushi. This "species" was mentioned briefly in his PhD dissertation (Modrý. 1998) but never published because oocysts were impossible to distinguish from *C. simplex/C. bigenetica* (Modrý, pers. comm.).

***Caryospora* sp. I of Šlapeta, Modrý, Ashe and Koudela, 2003**

Original host: Psammophis orientalis Broadley, 1977, eastern stripe-bellied sand snake (Colubridae).

Remarks: Šlapeta et al. (2003) found *Caryospora*-like oocysts in the feces of the only *P. orientalis* they examined from the Malindi area of coastal Kenya. They provided a very nice line drawing (their Fig. 10) and a photomicrograph

(their Fig. 5), along with a good, standard description of the sporulated oocyst. Ovoidal oocysts had a bilayered wall, ~1.5 thick, with the inner layer thinner than the outer; L × W (N = 30): 23.8 × 20.5 (22–25.5 × 19–22); L/W ratio: 1.2; M, OR, PG: all absent. Sporocysts were ovoidal, L × W (N = 30): 15.5 × 11.0 (15–16 × 10–12); L/W ratio: 1.4; SB: ellipsoidal, 2.5–3 × 1.0; SSB: ellipsoidal, 3–3.5 × 1.5; SR: small globules, < 1.0 wide, arranged tightly in center of sporocyst between SZs; SZ: banana-shaped, transversally striated. Šlapeta et al. (2003, Table 1) compared the oocysts of this form to 4 other *Caryospora* described from *Psammophis* but neglected to provide a binomial name for it. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

Caryospora sp. II of Šlapeta, Modrý, Ashe and Koudela, 2003

Original host: Psammophis orientalis Broadley, 1977, eastern stripe-bellied sand snake (Colubridae).

Remarks: Šlapeta et al. (2003) found other *Caryospora*-like oocysts in the feces of the only *P. orientalis* they examined from the Malindi area of coastal Kenya. They provided a very nice line drawing (their Fig. 11) and 2 photomicrographs (their Figs. 6, 7), along with a good, standard description of the sporulated oocyst. Ovoidal oocysts had a bilayered wall, ~2.0 thick, with a thicker outer layer that is slightly pitted and a thinner inner layer; L × W (N = 30): 33.6 × 27.6 (32–36 × 26–30); L/W ratio: 1.2 (1.1–1.4); M, OR, PG: all absent. Sporocysts were ovoidal, L × W (N = 30): 19.8 × 13.9 (18–21 × 13–14); L/W ratio: 1.4 (1.3–1.5); SB: ellipsoidal, 3.0 × 1.0; SSB: ellipsoidal, 3.5–4 × 1.5; SR: a few small globules, < 1.5 wide, scattered among SZs in center of sporocyst; SZ: banana-shaped, 1.5–2.0 wide, transversally striated and fill the sporocyst. Šlapeta et al. (2003, Table 1) compared the oocysts of this form to 4 other *Caryospora* described from *Psammophis* but neglected to provide a binomial name for it. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

Caryospora sp. of Upton and Sundermann, 1990

Original host: Bothriechis lateralis Peters, 1862, coffee-palm or yellow-lined pit viper (Viperidae).

Remarks: The authors mentioned only that they saw a caryosporan in this snake. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

Caryospora zuckermanae of Bray 1960

Original host: Hemorrhois ravergieri Ménétries, 1832 (syn. *Coluber ravergieri nummifer* Reuss, 1843), spotted whip snake (Colubridae).

Remarks: In 1960, Dr. Avivah Zuckerman sent Dr. Bray sections of the gut of a whip snake from Israel and gave him a brief description of the oocysts of a caryosporan he had seen, saying it was 16.7 (15–18) wide and "possessing an outer wall which resembles crumpled cellophane." Bray (1960) then described immature and mature gametocytes and meronts he found in the proximal end of epithelial cells from the tissue sections. He also provided very modest line drawings of these stages (Bray's Figs. 22–27), but he never saw sporulated oocysts, and neither he nor Zuckerman described such, and no one has found or mentioned this form since its initial mention by Bray (1960). I believe this form can only be called a *species inquirenda*.

Characterization of Eumonospora *Allen, 1933*

Chou et al. (2020) resurrected this genus from *Caryospora* for those species described to have oocysts with 1 sporocyst lacking both SB and SSB, as per Allen (1933), and that single sporocyst contains 8 SZ. Species are facultatively or obligatorily heteroxenous with indirect life cycles involving rodents as secondary hosts (to date, demonstrated only in the laboratory). The primary hosts are usually birds, mainly raptors.

Eumonospora *species in birds (23)*

Eumonospora (= _C._) _aquilae_ (Volf, Koudela, and Modrý, 2000) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Type host: Aquila chrysaetos (L., 1758), golden eagle (Accipitridae).

Other hosts: None to date.

Type locality: Czech Republic: Cheb, a long-term captive of zoos and rehabilitation centers in the country.

Sporulated oocyst: Subspheroidal to broadly ellipsoidal; number of walls: 2, ~2.2 (2.0–2.5) thick; wall characteristics: outer is smooth, inner, ~0.5 thick; L × W (N = 30): 43.0 × 37.5 (40–49 × 34–39); L/W ratio: 1.15 (1.0–1.3); M, OR, PG: all absent.

Sporocyst and sporozoites: Spheroidal to subspheroidal; L × W (N = 30): 23.8 × 23.3 (23–25 × 22–25); L/W ratio: 1.1 (1.0–1.4); SB, SSB, PSB: all absent; SR: present; SR characteristics: numerous small granules, < 0.5 wide, disbursed among SZs; SZ: vermiform, L × W (N = 30): 13.5 × 4.5 (13–14 × 4–5), each with a spheroidal posterior RB, ~3.0 wide.

Prevalence: Volf et al. (2000) found this species in the feces of only 1/10 (10%) golden eagles they examined from a private collection in Cheb, CR.

Sporulation: Exogenous. About 90% of the oocysts were sporulated within 3 days in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution at room temperature (~23°C).

Remarks: Volf et al. (2000) compared size and structures of the sporulated oocysts of this species to those of 10 previously described caryosporans from accipitrid and falconid birds of prey. Because its oocysts are larger than those described from any accipitrids, they concluded it could not be the same as any of those species. When compared to the sporulated oocysts from falconids, those of *E.* (*C.*) *aquilae* were similar in size to those of *E.* (*C.*) *metafalconis* Klüh, 1994. Klüh (1994) reported his species from 3 *Falco* species, but oocysts of *E.* (*C.*) *metafalconis* differed from those of *E.* (*C.*) *aquilae* in oocyst walls, sporocysts and SZ sizes, all characters that seemed to clearly distinguish one from the other.

Eumonospora (= *C.*) *arcayae* (Volcán and Medrano, 1984) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Synonym: Caryospora sp. of Upton and Sundermann, 1990.
Type host: Rupornis magnirostris (Gmelin, J.F., 1788) (syns. *Falco magnirostris* Gmelin, J.F., 1788; *Buteo magnirostris* [Gmelin, J.F., 1788]), roadside hawk (Accipitridae).

Other hosts: Buteo platypterus (Vieillot, 1823), broad-winged hawk (Accipitridae).

Type locality: Venezuela: State of Bolívar, Heres District.

Sporulated oocyst: Ovoidal; number of walls: 2, ~3 thick; wall characteristics: outer wall lightly pitted, 1.0–2.0 thick, inner layer smooth, 0.6–0.8 thick, slightly darker than outer layer; L × W: 32.9 × 29.4 (Volcán and Medrano, 1984) or L × W (N = 30): 32.1 × 28.3 (29–36 × 26–30); L/W ratio: 1.1 (1.1–1.2); M, OR, PG: all absent (Upton, Campbell, et al., 1990).

Sporocyst and sporozoites: Spheroidal, rarely subspheroidal; L × W: 21.9 × 21.8 (Volcán and Medrano, 1984) or L × W (N = 30): 20.0 (18–21); L/W ratio: 1.0; SB, SSB, PSB: all absent; SR: present; SR characteristics: numerous granules scattered among SZs in sporocyst, many of which seem to adhere to the inner surface of the sporocyst wall; SZ: described by Upton, Campbell, et al. (1990) as "stout" and measured, L × W: 12.0 × 5.1 (10–14 × 5–6), each with anterior transverse compression lines and 1, rarely 2, spheroidal RBs located either anterior or posterior to the large N (Upton, Campbell, et al., 1990).

Prevalence: Volcán and Medrano (1984) found unsporulated oocysts in 4/4 (100%) hawks they examined, and Upton et al. (1990) found oocysts that were indistinguishable from those described by Volcán and Medrano (1984) in the only *B. platypterus* they examined.

Sporulation: Exogenous. Sporulation occurred within 7 days at 23°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution (Upton, Campbell, et al., 1990).

Remarks: Upton, Campbell, et al., (1990) said that the oocysts they found in *B. platypterus* in Kansas (USA), "so closely resembled *C. arcayae* . . . that we consider the 2 forms synonyms."

Eumonospora (= *C.*) *argentati* (Schwalbach, 1959) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Type host: Larus argentatus Pontoppidan, 1763, European herring gull (Laridae).

Other hosts: None to date.

Type locality: Germany.

Sporulated oocyst: Pear-shaped (line drawing, Plate 27, Fig. 6, p. 493); number of walls: 1, 0.8–1.0 thick; wall characteristics: smooth outer layer; L × W: 20.3 × 16.9 (18.5–24 × 15–20.5); L/W ratio: 1.2; M, OR: both absent; PG: 1, adjacent to inner surface of the oocyst wall at the narrow end of the oocyst.

Sporocyst and sporozoites: Spheroidal (line drawing); L × W: dimensions not given in original description; SB, SSB: both absent; SR: a central compact mass of small granules; SZ: sausage-shaped, curled around granules (line drawing) of SR; RB: not observed, but a central N was depicted.

Prevalence: Schwalbach (1959) reported in his first table (p. 437) that 31/122 (25%) *L. argentatus* examined were infected with coccidia, but it was uncertain how many of the infected birds had *Caryospora* oocysts in their feces.

Sporulation: Exogenous. Sporulation occurred within 30 hours at 16°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: The only other mention of this form I could find in the literature was a paper by Frank (1978) who examined blood and/or fecal samples and made some very superficial observations on the protozoan fauna of 83 birds of eastern Austria. She (1978) found 1/2 (50%) *L. argentatus* "slightly infested" with pear-shaped oocysts of *E.* (*C.*) *argentati*; the oocysts were located in the rectum, and she said the integrity of the infected organ was unchanged. The oocysts she measured were 20 × 17, and she said they took 20 hours to sporulate completely.

Eumonospora (= *C.*) *biarmicusis* (Alyousif, Alfaleh and Al-Shawa, 2011) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Type host: Falco biarmicus Temminck, 1825, lanner falcon (Falconidae).

Other hosts: None to date.

Type locality: Saudia Arabia: Riyadh City, from the falcon market.

Sporulated oocyst: Ovoidal; number of walls: 2, 3.2 (3–5) thick; wall characteristics: smooth, brownish yellow; L × W (N = 30): 40.2 × 34.7 (37.5–42 × 33–36); L/W ratio: 1.2 (1.1–1.3); M, PG: both absent; OR: present, spheroidal, 10.3 (10–11) wide, consisting of many coarse granules.

Sporocyst and sporozoites: Spheroidal; L × W (N = 30): 20.1 (19–21); L/W ratio: 1.0; SB, SSB, PSB: all absent; SR: present; SR characteristics: numerous scattered granules, many of which line up along the inside of the sporocyst wall; SZ: stout, L × W (N = 30): 12.1 × 5.4 (10.5–14 × 5–6), each with faint transverse striations anteriorly, and a large, spheroidal posterior RB, ~3.0.

Prevalence: Alyousif et al. (2011) found this species in 2/40 (5%) fecal samples taken from individually caged *F. biarmicus* from the falcon market.

Sporulation: Exogenous. Sporulation occurred within 60–84 hours at 24°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: Alyousif et al. (2011) based their description of this form mainly on the details of oocyst structure (their Table 1, p. 5) and on geographic distribution (all of Europe) of the other 6 caryosporans described in the literature from other Falconidae species.

Eumonospora (= *C.*) *boeri* (Klüh, 1994) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Synonym: Caryospora sp. Kutzer, Frey and Kotremba, 1980.

Type host: Falco tinnunculus L., 1758, European kestrel (Falconidae).

Other hosts: None to date.

Type locality: Germany: Hannover.

Sporulated oocyst: Subspheroidal; number of walls: 2; wall characteristics: outer layer smooth, ~1.4 thick; L × W (N = 1,000): 36.6 × 33.4 (32–40 × 31–37); L/W ratio: 1.1; M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal; L × W (N = 1,000): 27.8 × 19.6 (26–31 × 18–21); L/W ratio: 1.4 (1.2–1.5); SB, SSB, PSB: all absent; SR: present; SR characteristics: spheroidal body, 16.6 (14–19); SZ: elongated , L × W: 16.6 × 4.7 (15–17 × 4–5); no SZ features (striations, RB, N) were mentioned in original description by Klüh (1994).

Prevalence: Klüh (1994) reported this species in 7/15 (47%) *F. tinnunculus*.

Sporulation: Exogenous. Sporulation was completed within 52–59 hours at 21°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution (Klüh, 1994).

Remarks: Mateuta and Samour (2017) surveyed 3,975 fecal samples from 6 falcon species plus 2 hybrid species in the United Arab Emirates and reported 297 (7.5%) positive for oocysts of *Caryospora*-like species; 2/297 (0.6%) were infected with *E.* (= *C.*) *boeri*. Their (2017) *E.* (= *C.*) *boeri* oocysts measured L × W: 38.5 × 31.0 (39 × 30–32), and sporocysts were L × W: 24.5 × 20.5 (24–25 × 20–21); SZ: L × W: 19.0 × 3.5 (18–20 × 3–4). From the data presented by Mateuta and Samour (2017), it was not possible to determine which host species/hybrids were infected by *E.* (= *C.*) *boeri*, nor the prevalence of infections in those infected.

Eumospora (= *C.*) *bubonis* (Cawthorn and Stockdale, 1981) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Type host: Bubo virginianus (Gmelin, 1788), great horned owl (Strigidae).

Other hosts: Bubo bubo (L., 1758), Eurasian eagle owl (Strigidae).

Type locality: Canada: Saskatchewan, Saskatoon.

Sporulated oocyst: Subspheroidal; number of walls: 2, ~1.1 thick; wall characteristics: outer layer, delicate, colorless, thicker, while inner layer is darker; L × W: 43.9 × 40.2 (38–52 × 33–47); L/W ratio: 1.1 (1.0–1.3); M, OR, PG: all absent.

Sporocyst and sporozoites: Subspheroidal; L × W: 26.6 × 25.6 (20–33 × 20–32); L/W ratio: 1.1 (1.0–1.2); SB, SSB, PSB: all absent; SR: present; SR characteristics: diffuse granules scattered among SZs; SZ: banana- or sausage-shaped (line drawing), L × W (N = 26): 15.5 × 2.5 (13–21 × 2–3), each with a central, spheroidal RB.

Prevalence: Unknown for Canada. Feces were collected from owls submitted for case study to the Small Animal Clinic, Department of Veterinary Clinical Studies, and from necropsies in the Department of Veterinary Pathology, Western College of Veterinary Medicine, University of Saskatchewan, Canada. Cawthorn and Stockdale (1981) neglected to mention the total number of owls that were infected or those examined for this caryosporan. Cardozo et al. (2019) reported finding *E.* (*C.*) *bubonis* in the only specimen of *B. bubo* they examined for coccidia in Portugal.

Sporulation: Exogenous. Sporulation occurs as early as 72 hours at 19–23°C in 2.5% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: In addition to finding and describing *E.* (= *C.*) *bubonis* (Cawthorn and Stockdale, 1981), the authors also did cross-transmission studies with various hosts and looked for endogenous developmental stages in owl intestines (Stockdale and Cawthorn, 1981; Cawthorn and Stockdale, 1982). These studies (1981, 1982) reported 2 types of meronts and their merozoites, both micro- and macrogamonts, and unsporulated oocysts in a subnuclear location of villar epithelial cells in the posterior one-third of the small

intestine in owls experimentally inoculated with oocysts. The prepatent period was 11.5–12.5 DPI, and patency lasted 4–11 days. Oocysts were not infective to the long-eared owl, *Asio otus* (L., 1758); short-eared owl, *Asio flammeus* (Pontoppidan, 1763); or to domestic chicks, *Gallus domesticus* (L., 1758). In mice (*Mus musculus* L., 1758) fed from 2.5 × 10^4 or 1.25 × 10^5 oocysts of owl origin 4 weeks previously, no stages of *E.* (= *C.*) *bubonis* were identified. However, a granuloma containing giant cells and mononuclear cells was seen in the liver of a mouse fed 25,000 *E.* (= *C.*) *bubonis* oocysts (Stockdale and Cawthorn, 1981). In other experimental mice, pyogranulomas, associated with phlebitis, developed mainly in the liver, although similar lesions were sometimes found in lung and brain, and giant cells were prominent. Similar lesions were found in mice used for indirect transmission studies (Cawthorn and Stockdale, 1982). In owls fed mice inoculated with oocysts of *E.* (= *C.*) *bubonis* 4 weeks previously, the prepatent period was shortened by 48 hours, which suggested to them (1982) that *E.* (= *C.*) *bubonis* can be transmitted both directly and indirectly via rodents in nature. It is interesting to note that no clinical signs were ever observed in any experimental owls infected with *E.* (= *C.*) *bubonis* oocysts.

Cardozo et al. (2019) examined feces from 89 wild birds, at 2 bird rehabilitation centers in Portugal, for coccidia. The birds represented 9 orders, 11 families, 17 genera, and 18 species of which 22/89 (25%) had coccidian oocysts. After measuring and photographing sporulated oocysts, Cardozo et al. (2019) identified *E.* (*C.*) *bubonis* in the only specimen of *B. bubo* in their survey.

Eumonospora (= *C.*) *cherrughi* (Alfaleh, Alyousif, Al-Shawa and Al-Quraishy, 2012/2013) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Type host: Falco cherrug Gray, J. E., 1834, saker falcon (Falconidae).

Other hosts: None to date.

Type locality: Saudi Arabia: Riyadh City, taken at the falcon market.

Sporulated oocyst: Ovoidal to subspheroidal; number of walls: 2, ~3.2 (3–5) thick; wall characteristics: outer layer brownish yellow, thicker, while inner layer is darker; L × W (N = 30): 32.1 × 29.3 (31–34.5 × 28–30); L/W ratio: 1.1 (1.0–1.3); M, OR, PG: all absent.

Sporocyst and sporozoites: Ellipsoidal; L × W (N = 30): 24.0 × 20.0 (23–26 × 19–21); L/W ratio: 1.2; SB, SSB, PSB: all absent; SR: present; SR characteristics: numerous scattered granules, many aligned along the inside of the sporocyst wall; SZ: banana-shaped, 15.0 × 4.0, each with faint transverse striations and a large spheroidal RB at its more rounded end.

Prevalence: Alfaleh et al. (2013) found that 15/70 (21%) saker falcons were passing caryosporan oocysts.

Sporulation: Exogenous. The majority of oocysts seen by Alfaleh et al. (2013) had completely sporulated within 64–84 hours at 24°C when placed in a thin layer of 2.5% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: Alfaleh et al. (2013) compared their sporulated oocysts to those of 7 other caryosporans described previously from other members of the Falconidae (Table 1, p. 973). They argued that their oocysts were easily distinguished from those of *E.* (*C.*) *falconis* by the shape of their oocysts and sporocysts. They also noted that the oocysts of their species differed from those of *E.* (*C.*) *boeri*, *E.* (*C.*) *biarmicusis*, *E.* (*C.*) *kutzeri*, and *E.* (*C.*) *megafalconis* by having much smaller oocysts and sporocysts. They pointed out several other minor structural differences in addition to the differences in host species of the other caryosporans.

Mateuta and Samour (2017) surveyed 3,975 fecal samples from 6 falcon species plus 2 hybrid species in the United Arab Emirates and reported 297 (7.5%) positive for oocysts of *Caryospora*-like species: 11/297 (4%) were infected with *E.* (*C.*) *cherrughi*. Their (2017) *E.* (*C.*) *cherrughi* oocysts measured L × W: 33.7 × 28.0 (23–35 × 23–32) and sporocysts were L × W: 22.6 × 18.9 (20–25 × 15–22); SZ: were L × W: 15.0 × 4.0 (12–20 × 3–5). From the data presented by Mateuta and Samour (2017), it was not possible to determine which host species/hybrids were infected by *E.* (*C.*) *cherrughi*, nor the prevalence of infections in those infected.

Eumonospora (= *C.*) *circi* (Volf, Koudela and Modrý, 2000) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Type host: Circus aeruginosus (L., 1758), western marsh harrier (Accipitridae).

Other hosts: None to date.

Type locality: Czech Republic: Frýdek-Místek District, Rychaltice.

Sporulated oocyst: Ovoidal; number of walls: 2, ~2 thick; wall characteristics: outer is smooth, colorless, with inner layer ~0.5 thick; L × W (N = 30): 24.5 × 21.8 (23–25 × 21–24); L/W ratio: 1.1 (1.0–1.2); M, OR, PG: all absent.

Sporocyst and sporozoites: Spheroidal to subspheroidal; L × W (N = 30): 16.2 × 15.6 (15–17 × 15–17); L/W ratio: 1.0 (1.0–1.1); SB, SSB, PSB: all absent; SR: present; SR characteristics: spheroidal to subspheroidal mass of granules, L × W (N = 30): 10.4 × 8.5 (10–11 × 7–9), in 76% of the sporocysts while in the other 24% the SR appeared as a mass of scattered granules; SZ: elongate ovoidal forms with transverse striations and measured, L × W (N = 30): 10.4 × 4.3 (9–11 × 4–5); each SZ with a central, spheroidal N.

Prevalence: Volf et al. (2000) found this species in 1/13 (8%) marsh harriers they examined.

Sporulation: Exogenous. Most oocysts had completely sporulated within 4 days at 23°C when placed in a thin layer of 2.5% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: Among caryosporans that infect accipitrid birds, the sporulated oocysts of *E.* (*C.*) *circi* seem most similar to those of *E.* (*C.*) *uptoni* but differ by having significantly smaller sporocysts; all the known caryosporans that infect all other accipitrids have larger oocysts and sporocysts. Of the caryosporan species of falconid raptors, the oocysts of *E.* (*C.*) *circi* are only similar to those of *E.* (*C.*) *neofalconis*, but its oocysts and sporocysts are also much smaller.

Eumonospora (= *C.*) *daceloe* (Yang, Brice and Ryan, 2014) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Type host: Dacelo novaeguineae (Hermann, 1783), laughing kookaburra (Alcedinidae).

Other hosts: None to date.

Type locality: Australia: Western Australia, Perth, Leeming (32.0820°S, 115.8510°E).

Sporulated oocyst: Ovoidal; number of walls: 2; wall characteristics: smooth, colorless; L × W (N = 30): 31.4 × 29.3 (30–32 × 28–31); L/W ratio: 1.05 (1.0–1.1); M, OR, PG: all absent.

Sporocyst and sporozoites: Sporocyst shape: Spheroidal to subspheroidal; L × W (N = 30): 21.2 × 20.6 (20–24 × 20–21); L/W ratio: 1.03 (1.0–1.1); SB, SSB: both absent; SR: present; SR characteristics: mostly spheroidal composed of a compact mass of globules; SZ: vermiform, L × W (N = 30): 17.0 × 4.8 (16–18 × 4–6), each with a large RB in the middle of the SZ.

Prevalence: This species was detected in 2/30 (6.7%) samples from *D. novaeguineae* collected in the morning and from 3/9 (33%) samples collected in the afternoon (Yang et al., 2014).

Sporulation: Unknown. Yang et al. (2014) assumed the sporulation to be 48–72 hours in 2% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution at room temperature.

Remarks: The laughing kookaburra is a carnivorous bird and the largest member of the kingfisher family, Alcedinidae (syn. Halcyonidae). When *E.* (*C.*) *daceloe* was described (Yang et al., 2014), a *Caryospora* species had been identified in only 1 other native Australian bird, the tawny frogmouth, *Podargus strigoides* (Latham, 1801), which had been reported to suffer severe disease (Montali et al. 2005; however, to my knowledge, the information in this abstract, from an international conference in Cairns, was never published in a juried article). In the abstract by Montali et al. (2005), oocysts from the tawney frogmouth were reported as spheroidal to subspheroidal and measured 28–34 × 28–32 with ovoidal sporocysts that measured 19–24 × 18–23. Other than size discrepancies, the main morphological difference between the 2 forms was the presence of the large spheroidal RB in the SZ of *E.* (= *C.*) *daceloe*, not reported by Montali et al. (2005); this convinced Yang et al. (2014) that their form was a different species than the 1 seen by Montali et al. (2005), which the latter authors did not name.

Yang et al. (2014) obtained 3 identical, nearly full-length sequences of the 18S rRNA gene from their oocysts. These were aligned with 2 *Caryospora bigenetica* sequences (Clones 1 and 2) in GenBank and their phylogenetic analysis using distance, parsimony, and maximum likelihood showed that *E.* (= *C.*) *daceloe* exhibited 99.2% similarity with *Besnoitia* and 98.8% similar to *Hammondia*, while there was only an 89% similarity between *E.* (= *C.*) *daceloe* and *C. bigenetica*.

Eumonospora (= *C.*) *falconis* (Wetzel and Enigk, 1937) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Type host: Falco peregrinus L., 1758, peregrine falcon (Falconidae).

Other hosts: Falco subbuteo L., 1758, Eurasian hobby; *Falco tinnunculus* L., 1758, European kestrel (both Falconidae); *Athene noctua* (Scopoli, 1769), little owl (Strigidae).

Type locality: Germany.

Sporulated oocyst: Spheroidal; number of walls: 1 (line drawing); wall characteristics: smooth, colorless, thin; L × W: 32–34 wide; L/W ratio: 1.0; M, OR, PG: all absent.

Sporocyst and sporozoites: Subspheroidal (line drawing); L × W: 21–23 wide (no other measurements given); L/W ratio: unknown; SB, SSB, PSB: all absent; SR: present; SR characteristics: mostly a spheroidal mass of compact granules enclosed by the SZs; SZ: described as, "whetstone-shaped" (Wetzel and Enigk, 1937, p. 7); SZ: surround the SR and are 13–14 long.

Prevalence: Unknown.

Sporulation: Exogenous. Sporulation takes 3 days at room temperature (Wetzel and Enigk, 1937).

Remarks: Wetzel and Enigk (1937) noted that sometimes the sporocyst wall ruptures so that only 8 free SZ are seen within the oocyst wall. By any standard, the original description of this species is marginal, with only a few measurements of a few structures; the only reason for not relegating this to a *species inquirenda* is the authors did provide a small (2 cm), primitive line drawing. From that modest drawing, Lindsay and Blagburn (1986) estimated that the sporocysts are about 25 wide. Wetzel and Enigk

(1937) reported that *A. noctua* could be experimentally infected with *E.* (= *C.*) *falconis*, but these results have been considered to be in error by Volf et al. (2000) and others (Upton, Campbell, et al., 1990; Afaleh et al., 2013). However, Wetzel and Enigk (1939) stated again (in a popular magazine article) that *E.* (= *C.*) *falconis* "was not faithful to its host" (p. 31) because it was possible for them to transfer it to the little owl.

Cardozo et al. (2016) list oocyst dimensions as 29.5 × 36.5 (their Table 2, p. 205), but this is likely a *lapsus calami* when they meant to say 29.5–36.5 wide. Mateuta and Samour (2017) surveyed 3,975 fecal samples from 6 falcon species plus 2 hybrid species in the United Arab Emirates and reported 297 (7.5%) positive for oocysts of *Caryospora* species: 31/297 (10%) were infected with *E.* (= *C.*) *falconis*. Their (2017) *E.* (= *C.*) *falconis* oocysts measured L × W: 32.4 × 29.8 (29–36 × 23–35); sporocysts were L × W: 21.7 × 20.6 (15–25 × 14–25); and SZs were L × W: 13.2 × 4.6 (10–17 × 2–4). From the data presented by Mateuta and Samour (2017), it was not possible to determine which host species/hybrids were infected by *E.* (= *C.*) *falconis*, nor the prevalence of infections in those infected.

***Eumonospora* (= *C.*) *gloriae* (Pellérdy, 1967) n. comb.**

Type host: Ptiloxena atroviolacea (d'Orbigny, 1839) (syn. *Dives atroviolaceus*), Cuban blackbird or toti (Icteridae).

Other hosts: None to date.

Type locality: Cuba: Havana, National Zoo of Cuba.

Sporulated oocyst: Ovoidal; number of walls: 1 (line drawing); wall characteristics: smooth, colorless, thin, sometimes irregularly dented during processing; L × W: 32 × 28; L/W ratio: 1.1; M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal (line drawing); L × W: 28 × 20; L/W ratio: 1.4 (no other measurements given); SB, SSB, PSB: all absent; SR: present; SR characteristics: mostly spheroidal (line drawing) and Pellérdy (1967) said it had similar dimensions to the SZ; SZ: described as "rounded-ovoid bodies" (1967, p. 229), but they have no defined internal structures in either the line drawing (Fig. 1c, p. 228) or in the text description.

Prevalence: Found in the only specimen of the toti examined by Pellérdy (1967); this bird also was infected with a species of *Isospora* that he (1967) also described as new.

Sporulation: Exogenous. At 4 days after collection of feces, no sporulated oocysts were seen, but at 9 days "completely sporulated oocysts were apparent in the culture" (1967, p. 230), presumably at room temperature (?).

Remarks: Pellérdy (1967) screened about 50 species of birds in the Havana zoo and found only 2 birds shedding coccidian oocysts. In his description of this species, he said, "In the sporulated oocysts a single sporocyst is apparent. It is tapering towards one end, where the presence of a micropyle [i.e., SB] is suspected" (1967, p. 228). Unfortunately, Pellérdy (1967) did not include a photomicrograph of the oocyst and his line drawing shows only a tiny point at one end of the sporocyst, not a definitive SB. My conclusion is that a SB/SSB complex is not present, and that this species must be reassigned to *Eumonospora*.

***Eumonospora* (= *C.*) *hanebrinki* (McAllister, Duszynski and McKown, 2013a) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020**

Type host: Haliaeetus leucocephalus (L.,1766), bald eagle (Accipitridae).

Other hosts: None to date.

Type locality: USA: Kansas, Finney County, somewhere near Garden City (37.5831°N, 100.5151°W).

Sporulated oocyst: Ovoidal to ellipsoidal; number of walls: 2, ~2.0 thick; wall characteristics: outer layer, smooth to textured, ~1.4, inner layer, 0.6; L × W (N = 30): 48.1 × 42.1 (42–54 × 37–50); L/W ratio: 1.2 (1.0–1.4); M, OR, PG: all absent.

Sporocyst and sporozoites: Spheroidal; L × W (N = 30): 24.8 (23–28); L/W ratio: 1.0; SB, SSB, PSB: all absent; SR: present; SR characteristics: spheroidal mass, 17.5 (16–20) wide, composed of a ball of tiny granules with many homogeneous globules disbursed in a spiral around the SR; SZ: banana-shaped (line drawing), L × W (N = 30): 18.6 × 5.6 (16–20 × 4–6), each SZ with faint vertical striations and 2 spheroidal RBs.

Prevalence: This species was found in 1/4 (25%) specimens of the type host.

Sporulation: Exogenous. Sporulation was completed in 4 days when placed in 2.5% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution at room temperature.

Remarks: This species demonstrates some of the largest sporulated oocysts known from all raptors, although sporulated oocysts and their sporocysts from a few other raptors approach the sizes of *E.* (= *C.*) *hanebrinki*, including *E.* (= *C.*) *bubonis* from *B. virginianus* (oocyst 44 × 40; sporocyst 27 × 26), *E.* (= *C.*) *aquilae* from *A. chrysaetos* (43 × 37.5; 24 × 23), *E.* (= *C.*) *henryae* from *B. bubo* (41 × 37; 23.5 × 21), *E.* (= *C.*) *biarmicusis* from *F. biarmicus* (40 × 35; 20 wide), and *E.* (= *C.*) *megafalconis* from *F. rusticolus* (44 × 36; 24 wide). However, qualitative differences between oocyst and sporocyst features and geographic distances convinced McAllister et al. (2013a) their species was distinct from the others.

***Eumonospora* (= *C.*) *henryae* (emend. Pellérdy, 1974) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020**

Synonyms: Isospora henryi Yakimoff & Matikaschwili, 1932; *Eumonospora tremula* Allen, 1933; *Caryospora henryi* (Yakimoff & Matikaschwili, 1932) Yakimoff & Matschulsky, 1936; *Caryospora henryae* (Yakimoff & Matschulsky, 1936) Pellérdy, 1974.

Type host: Bubo bubo (L., 1758), Eurasian eagle-owl (Strigidae).

Other hosts: Athene noctua (Scopoli, 1769), little owl (Strigidae); *Bubo scandiacus* (L., 1758), snowy owl (Strigidae); *Cathares aura* (L., 1758), turkey vulture (Cathartidae); *Falco columbarius* L., 1758, merlin (Falconidae); *Falco* (*Tinnunculus*) *tinnunculus* L., 1758, common kestrel (Falconidae); *Falco subbuteo* L., 1758, Eurasian hobby (Falconidae); *Milvus migrans* (Boddaert, 1783), black kite (Accipitridae); *Ptilosis leucotis* (Temminck, 1820), northern white-faced owl (Strigidae); *Strix nebulosi* Foster, 1772, great gray owl (Strigidae).

Type locality: Russia: Leningrad, Zoological Gardens of Leningrad.

Sporulated oocyst: Ovoidal to spheroidal to subellipsoidal with dimensions that vary from host to host; number of walls: 3; wall characteristics: outer layer is greenish, the middle layer is brown, the inner layer was thickest, 3–6 thick; or, oocyst wall with only 2 layers (Chou et al., 2021); in **falcons**, ovoidal oocysts were L × W (N = 67): 36.5 × 32.1 (31–45 × 27–36); L/W ratio: 1.1; spheroidal oocysts were L × W (N = 12): 33.4 (31–36); L/W ratio: 1.0; and ellipsoidal oocysts were L × W: 40.4 × 34.3 (37–44 × 30.5–38); L/W ratio: 1.2; in **kites**, ovoidal oocysts were L × W (N = 46): 36.8 × 28.1 (31–45 × 27–36); L/W ratio: 1.1; spheroidal oocysts were, L × W: 35.3 (31–36); L/W ratio: 1.0; in **eagle-owls**, ovoidal oocysts were L × W (N = 15): 41 × 37 (40–43 × 36–40); L/W ratio: 1.1; spheroidal oocysts were, L × W: 36–38 wide; L/W ratio: 1.0; M, OR, PG: all absent.

Sporocyst and sporozoites: Spheroidal to subspheroidal; L × W: 20 × 20 (22–25 × 20–22); L/W ratio: 1.0; or, L × W: 23.0 × 22.6 (20–28 × 20–28); L/W ratio: 1.0; SB, SSB, PSB: all absent; SR: present; SR characteristics: concentrated as a single mass of granules (line drawing) or scattered in sporocyst; SZ: tadpole-shaped, L × W: 11–14 × 3–5; or ellipsoidal, L × W: 13.6 × 4.9 (11–17 × 4–6); L/W ratio: 1.1; 1 small RB at the rounded end of each SZ (line drawing).

Prevalence: Apparently, oocysts were found in the droppings of 1/1 *F. tinnunculus*, 3/3 *F. subbuteo*, 3/3 *M. migrans*, and 2/2 *B. bubo* examined by Yakimoff and Matikaschwili (1932) and Yakimoff and Matschulsky (1936). Chou et al. (2021) found large numbers of oocysts in the diarrheic stool of 1/1 (imported) *F. columbarius* in Japan.

Sporulation: Exogenous. Sporulation took about 96 hours in 2% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution at room temperature.

Remarks: Yakimoff and Matikaschwili (1932) described a coccidium found in the feces of *B. bubo* in the Leningrad Zoological Gardens based on only 5, ovoidal, flattened oocysts that measured 37–42 × 30–35 with a single spheroidal sporocyst that was 20 wide. They named their species *I. henryi*, assuming that these oocysts had not sporulated properly because the sporocysts contained 8 SZ. A few years later, they found oocysts with very similar structures in *F. tinnunculus*, *F. subbuteo*, and *M. migrans*, also from the Leningrad zoo (Yakimoff and Matschulsky, 1936); they discovered their error (1932) and called their species *C. henryi*. They also synonymized *Eumo. tremula* Allen, 1933 with their new species name. Pellérdy (1974) emended the specific epithet to reflect the female gender. Cawthorn and Stockdale (1982) did some cross-transmission work with this species and demonstrated rather narrow host-specificity, suggesting that more than 1 species may be involved in parasitizing these 4 families of predatory birds. Recently, however, Chou et al. (2021) using genomic datasets consisting of nuclear 18S rDNA, nuclear 28S rDNA, and mitochondrial cytochrome C oxidase subunit 1 gene sequences demonstrated a well-supported monophyletic clade of *Eumonospora* spp. belonging to the family Sarcocystidae that largely corresponded to the avian host phylogram. Using their phylogenetic analyses combined with oocyst morphology encouraged them to create a new subfamily, Eumonosporinae within the Sarcocystidae. Thus, the question of host specificity by *E. henryae* in predatory birds is still open for debate. Some authors (Allen, 1933; Böer, 1982; Cawthorn and Stockdale, 1982) who did experimental cross-transmission studies were unable to transmit it between multiple avian species, while others (Yakimoff and Matikaschwili, 1932; Wetzel and Enigk, 1937; Klüh, 1994; Schuster et al., 2016; Chou et al., 2020) have either been successful or have indicated that some *Eumonospora* spp. may display a wide host spectrum. Among all members of the *Eumonospora*, *Eum. henryae* is the most taxonomically confusing species.

***Eumonospora* (= *C.*) *kansasensis* (Upton, Campbell, Wiegel and McKown, 1990a) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020**

Synonym: Caryospora sp. of Upton and Sundermann, 1990.

Type host: Buteo swainsoni Bonaparte, 1838, Swainson's hawk (Accipitridae).

Other hosts: None to date.

Type locality: USA: Kansas.

Sporulated oocyst: Ovoidal; number of walls: 2, ~2.0 thick; wall characteristics: outer is colorless, smooth, ~1.4 thick; inner layer is smooth, ~0.6; L × W (N = 30): 37.2 × 32.6 (33–40 × 30–36); L/W ratio: 1.1 (1.1–1.2); M, OR, PG, all absent.

Sporocyst and sporozoites: Spheroidal; L × W (N = 30): 22.5 (21–25); L/W ratio: 1.0; SB, SSB, PSB: all absent; SR: present; SR characteristics: numerous granules scattered throughout sporocyst, sometimes lined along the inside of sporocyst wall; SZ: Upton et al. (1990) said SZ were "stout," L × W (N = 30): 14.4 × 5.4 (14–17 × 5–6), each with anterior transverse striations, a large posterior N, and 1 RB usually anterior to the N.

Prevalence: Upton, Campbell, et al. (1990) found this species in 1/4 (25%) specimens of the type host examined.

Sporulation: Exogenous. Sporulation occurred within 7 days at 23°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution (Upton, Campbell, et al., 1990).

Remarks: The sporulated oocysts of this species are similar to those of *E.* (*C.*) *kutzeri* but are smaller and more elongated, and their sporocysts are spheroidal rather than ellipsoidal. These oocysts also are somewhat similar to those of a *Car.* sp. found in *Milvus migrans* by Yakimoff and Matschulsky (1936) but differ by having larger and more spheroidal oocysts and possessing spheroidal rather than ellipsoidal sporocysts (Upton, Campbell, et al., 1990).

Eumonospora (= *C.*) *kutzeri* (Böer, 1982) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Synonym: Caryospora henryi of Yakimoff and Matschulsky, 1936, in part; *Caryospora* sp. of Kutzer, Frey and Kotremba, 1980; *Caryospora falconis* of Scheller and Rodler, 1971.

Type host: Falco mexicanus Schlegel, 1850, prairie falcon (Falconidae). Although Böer (1982) did not identify the type host, it is the first one he mentioned in which he found the infection with this species, so I've designated it as such.

Other hosts: Bubo scandiacus (syn. *Nyctea scandiaca*) (L., 1758), snowy owl (Strigidae); *Falco biarmicus* Temminck, 1825, lanner falcon (Falconidae); *Falco cherrug* Gray, J.E., 1834, saker falcon (Falconidae); *Falco columbarius* L., 1758, merlin (Falconidae); *Falco jugger* Gray, J.E., 1834, laggar falcon (Falconidae); *Falco peregrinus* Tunstall, 1771, peregrine falcon (Falconidae); *Falco rusticolus* L., 1758, gyrfalcon (Falconidae); *Falco subbuteo* L., 1758, Eurasian hobby (Falconidae); *Falco tinnunculus* L., 1758, European kestrel (Falconidae).

Type locality: Germany.

Sporulated oocyst: Spheroidal to subellipsoidal; number of walls: probably 2 (photomicrographs, Böer, 1982, Figs. 7–9, p. 44); wall characteristics: outer layer is colorless, smooth; L × W (N = 396): 38.7 × 34.1 (34–45 × 30–38); L/W ratio: 1.1; M, OR, PG, all absent. Cardozo et al. (2016, Table 2, p. 205) listed the oocysts of this species using Böer's (1982) measurements as L × W: 38.7 × 34.1.

Sporocyst and sporozoites: Subspheroidal; L × W: 24.6 × 21.0 (21–27 × 19–23.5); L/W ratio: 1.2; SB, SSB, PSB: all absent; SR: present; SR characteristics: a single mass of granules (photomicrograph, Böer, 1982, Figs. 8, 8a, p. 44) between SZs; SZ: stout, sausage-shaped, but no measurements or other details were given.

Prevalence: Böer (1982) found this species in 1/11 (9%) *F. mexicanus*, in 1/45 (2%) *F. biarmicus*, in 2/62 (3%) *F. cherrug*, in 1/58 (2%) *Falco jugger*, in 24/184 (13%) *F. perigrinus*, in 14/47 (30%) *F. rusticolus*, and in 1/44 (2%) *Falco tinnunculus*, but he did not find it in 5 *F. chiquera* or in 5 *F. subbuteo*. Volf and Modrý (1998) reported on their survey of fecal samples of 397 birds of prey from raptor rehabilitation centers, zoos, and private raptor keepers in the Czech Republic; they found oocysts of *E.* (= *C.*) *kutzeri* in 4/47 (8.5%) *F. cherrug,* in 3/26 (11.5%) *F. peregrinus*, and in 11/47 (23%) *F. tinnunculus*, but no measurements or other data were provided in their abstract.

Sporulation: Exogenous. Böer (1982) said that sporulation was completed in 3 days when maintained in potassium dichromate at 21°C.

Remarks: Böer (1982) said he was able to transmit this parasite to *F. biarmicus*, *F. tinnunculus*, *F. peregrinus*, and to *F. subbuteo*. He also tried transmission via lab mice (paratenic host) to *F. tinnunculus*; 1 of 3 birds discharged oocysts on days 10–12 PI, but the numbers were small and the results were doubtful and needed to be checked again (Klüh, 1994).

Schaffrath-Böer (1983) studied the endogenous cycle of *E.* (*C.*) *kutzeri* in 10 *F. tinnunculus* she inoculated with 100,000 to 250,000 sporulated oocysts and then killed 1 every 24 hours on 2 to 11 DPI. She examined the intestine, liver, spleen, lungs, kidneys, gizzard, proventriculus, and gallbladder for parasite stages. No developmental stages were found on 2–4 DPI. One kestrel killed on 5 DPI (infective dose, 100,000 oocysts) had merozoites in the posterior one-third of the small intestine; these measured L × W: 11.5 × 3.5 (10–13 × 3–4). No parasite stages were found on 6 and 7 DPI in birds infected with 100,000 oocysts. On 8 DPI, numerous endogenous stages again were found, and they were comparable in size to those seen on day 5 PI; some of these merozoites had 2 or more N, while others beside them had only 1 N. Mature meronts were never observed. On 9, 10, and 11 DPI, gamonts and oocysts were present besides merozoites throughout the small intestine. All parasite stages were localized in villus epithelial cells distal to the host cell N. Macrogametes measured L × W: 19.3 × 18.7 (12–30 × 10–26), but wall-forming bodies were never seen.

Ovoidal to bean-shaped microgamonts measured L × W: 18.6 × 13.0 (14–28 × 9–15) and contained 63–85 microgametes. No parasite stages were found in any of the extraintestinal tissues/locations examined. None of the kestrels showed any clinical signs or pathological lesions.

Klüh (1994) experimentally infected hawks with 1,000 oocysts each of *E.* (= *C.*) *megafalconis, E.* (= *C.*) *kutzeri,* and *E.* (= *C.*) *neofalconis* and determined that the prepatent time differed for each species; ~219 hours for *E.* (= *C.*) *megafalconis,* ~264 hours for *E.* (= *C.*) *kutzeri,* and ~271 hours for *E.* (= *C.*) *neofalconis*. Klüh (1994) also reviewed the literature on the discovery of this species. He pointed out that Boer (1982) assigned the name *E.* (= *C.*) *kutzeri* to the oocysts detected in kestrels and tree falcons by Yakimoff and Matschulsky (1936) when they examined birds from the Leningrad zoo. However, based on Klüh's (1994) results this seemed doubtful, as both the host birds and the oocyst sizes suggest the species was actually *E.* (= *C.*) *boeri*. However, since the Russian authors did not provide any information on sporocyst morphology, a definitive assignment of their oocysts to either *E.* (= *C.*) *kutzeri* or *E.* (= *C.*) *boeri* is not possible.

Pavlík et al. (1998) examined 91 birds of prey, representing 10 species, from the Falcon Breeding Facility in Milotíce, Czech Republic, and collected 430 fecal samples from them. They reported oocysts of *E.* (= *C.*) *kutzeri* and clinical signs (diarrhea, reduced food intake) in the following birds: in 6/25 (24%) *F. peregrinus* (peregrine falcon), and 1/6 (17%) infected birds showed clinical signs; in 1/39 (3%) *F. cherrug* (saker falcon), and the only infected bird showed clinical signs; in 2/2 (100%) *F. rusticolus* (gyrfalcon), neither of which showed clinical signs of infection; in 2/12 (17%) hybrids (*F. peregrinus* × *F. cherrug*), and 1/2 (50%) infected birds showed clinical signs. Pavlík et al. (1998) also recorded double infections with oocysts of both *E.* (= *C.*) *neofalconis* and *E.* (= *C.*) *kutzeri* found in 2/39 (5%) *F. cherrug* (saker falcon); in 1/2 (50%) *F. tinnunculus* (kestrel); and in 2/2 (100%) *F. subbuteo* (hobby falcon), none of which showed clinical signs of infection. Volf et al. (2001) fed various doses (10^3, 10^4, 10^5) of *E.* (= *C.*) *kutzeri* sporulated oocysts to 2 species of coccidia-free, laboratory-reared rodents, crossbred CD-1 (ICR) BR mice (*M. musculus*) and common voles (*Microtus arvalis* Pallas). The oocysts were collected from a naturally infected saker falcon (*F. cherrug*) from the Czech Republic. Two kestrels fed infected mice shed oocysts 6 DPI after ingesting infected mouse tissues. Two kestrels fed only sporulated oocysts became patent 8 and 9 DPI and continued to discharge oocysts for at least 25 more days. However, Volf et al. (2001) were unable to find any developmental stages in 28 different rodent tissues 18 DPI with *E.* (= *C.*) *kutzeri*. Their experiment showed that some developmental stage(s) of *E.* (= *C.*) *kutzeri* are able to survive in mouse tissues and cause infection in suitable hosts after their ingestion.

Mateuta and Samour (2017) surveyed 3,975 fecal samples from 6 falcon species plus 2 hybrid species in the United Arab Emirates and reported 297 (7.5%) positive for oocysts of *Caryospora* species; 123/297 (44%) were infected with *E.* (= *C.*) *kutzeri*. Their (2017) *E.* (= *C.*) *kutzeri* oocysts measured L × W: 39.1 × 33.1 (33–46 × 28–40); sporocysts were L × W: 22.5 × 21.3 (18–26 × 16–26); SZ: were 4.6 (2–7) long. From the data presented by Mateuta and Samour (2017), it was not possible to determine which host species/hybrids were infected by *E.* (= *C.*) *kutzeri*, nor the prevalence of infections in those infected.

Eumonospora (= *C.*) *lindsayi* (Upton, Campbell, Weigel and McKown, 1990a) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Type host: Buteo jamaicensis (Gemlin, 1788), red-tailed hawk (Accipitridae).

Other hosts: None to date.

Type locality: USA: Kansas.

Sporulated oocyst: Subspheroidal; number of walls: 2, ~1.8–2.0 thick; wall characteristics: outer layer relatively smooth, ~1.2 thick, inner layer is smooth, ~0.6–0.8 thick; L × W (N = 30): 33.7 × 31.6 (31–36 × 30–33); L/W ratio: 1.1 (1.0–1.2); M, OR, PG, all absent.

Sporocyst and sporozoites: Spheroidal; L × W (N = 30): 20.5 (19–22); L/W ratio: 1.0; SB, SSB, PSB: all absent; SR: generally present; SR characteristics: spheroidal body, 11.6 (10–14) wide in 90% of the sporocysts, while the granules are scattered in about 10% and, refractile granules are also found free in the sporocyst in addition to the residuum; SZ: Upton, Campbell, et al. (1990) said SZ were "stout," L × W (N = 30): 15.5 × 4.8 (14–17 × 4–5), each with faint anterior striations and a large posterior RB, 3.4 (3–4) wide; N usually not visible.

Prevalence: Upton, Campbell, et al. (1990) found this species in 1/8 (12.5%) specimens of the type host examined.

Sporulation: Exogenous. Sporulation occurred within 7 days at 23°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution (Upton, Campbell, et al., 1990).

Remarks: Sporulated oocysts of *E.* (= *C.*) *lindsayi* were described as most similar to those of *E.* (= *C.*) *arcayae*, but the latter are smaller and less spheroidal than those of *E.* (= *C.*) *lindsayi*. The only other species described from red-tailed hawks, *E.* (= *C.*) *uptoni*, has oocysts that are considerably smaller than those of *E.* (= *C.*) *lindsayi* (Upton, Campbell, et al., 1990).

***Eumonospora* (= *C.*) *megafalconis* (Klüh, 1994) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020**

Type host: Falco rusticolus L., 1758, gyrfalcon (Falconidae).

Other hosts: Falco cherrug Gray, J.E., 1834, saker falcon (Falconidae); ger-saker hybrid; *Falco peregrinus* Tunstall, 1771, peregrine falcon (Falconidae); *Falco tinnunculus* L., 1758, common or European kestrel (Klüh, 1994, experimentally) (Falconidae); *Chlamydotis macqueenii* (Gray, J.E., 1832), MacQueen's bustard (Otididae); *Chlamydotis undulata* (Jacquin, 1784), Houbara bustard (Otididae).

Type locality: Germany: University of Veterinary Medicine Hannover.

Sporulated oocyst: Subspheroidal or ovoidal; number of walls: 2, ~1.6 thick; wall characteristics: outer layer relatively smooth; L × W (N = 1,000): 43.6 × 35.8 (39–48 × 32–41); L/W ratio: 1.2 (1.1–1.4); M, OR, PG, all absent.

Sporocyst and sporozoites: Spheroidal; L × W (N = 1,000): 23.8 (22–24); L/W ratio: 1.0; SB, SSB, PSB: all absent; SR: present; SR characteristics: spheroidal body, 16.5 (16–17), with a few single granules scattered in the sporocyst; SZ: banana-shaped (photomicrograph), L × W: 18.6 × 4.6 (17–20 × 4–6); no sporocyst features (striations, RB, N) were mentioned in original description by Klüh (1994).

Prevalence: Klüh (1994) reported this species in 10/86 (12%) Falconidae samples including: 6 *F. rusticolus*, 2 *F. cherrug*, and in 2 ger-saker hybrids; he also was able to successfully infect 7/15 (47%) young *F. tinnunculus*. Schuster et al. (2016) reported that 679 bustards representing 8 species were received for necropsy at the Central Veterinary Research Laboratory (CVRL) in Dubai (United Arab Emirates [UAE]). Between 2005 and 2013, 5 wild-caught adult MacQueen's bustards were found to be shedding *Caryospora*-like oocysts. In 2004, identical oocysts were detected in the Hubara breeding center at CVRL in captive-bred Houbara bustards that originated in Morocco. In February 2014, 5/10 (50%) Houbara bustards were shedding caryosporan oocysts and 4 Houbara chicks died of cryptosporosis by April. In 2016, 9/42 (21%) apparently healthy Houbara chicks excreted caryosporan oocysts and macrogametes, and unsporulated oocysts were found in the anterior part of the small intestine and unsporulated oocysts were found throughout the entire intestine.

Sporulation: Exogenous. Sporulation was completed within 76–85 hours at 21°C in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution (Klüh, 1994). Schuster et al. (2014) said sporulation was completed in 48 hours when kept at 26°C in 2.5% $K_2Cr_2O_7$.

Remarks: Klüh (1994) experimentally infected hawks with 1,000 oocysts each of *E.* (= *C.*) *megafalconis, E.* (= *C.*) *kutzeri,* and *E.* (= *C.*) *neofalconis* and determined that the prepatent time differed for each species: ~219 hours for *E.* (= *C.*) *megafalconis,* ~264 hours for *E.* (= *C.*) *kutzeri,* and ~271 hours for *E.* (= *C.*) *neofalconis*.

One of the frustrations in summarizing published literature to assemble comprehensive datasets like this one are the *lapsus calami* made by previous authors. As just one example, Alfaleh et al. (2013) described *E.* (*C.*) *cherrughi* infecting *F. cherrug* in Saudi Arabia. In their discussion (p. 973), they correctly cited Klüh (1994) as having found and reported *E.* (= *C.*) *megafalconis* in *F. cherrug, F. rusticulus,* and *F. tinniculus* (experimentally). But on the same page (Table 1) they list the *Caryospora*-like species described to that date from Falconidae, and for *E.* (= *C.*) *megafalconis* they list its "hosts" as *F. biarmicus*, Lanner falcon; *F. mexicanus*, prairie falcon; *F. peregrinus*, peregrine falcon; and *F. subbuteo*, Eurasian hobby with no explanation where those host names originated.

Schuster et al. (2016) in Dubai (UAE) reported finding oocysts of *E.* (= *C.*) *megafalconis* in 2 species of bustards, *C. macqueenii* (MacQueen's) and *C. undulata* (Houbara), in a systematically distant host family (Otididae). These bustard parasites showed the same dimensions as *E.* (= *C.*) *megafalconis* oocysts from falcons (2016, Table 1, p. 4391). They (2016) used sporulated oocysts of *E.* (= *C.*) *megafalconis* and *E.* (= *C.*) *neofalconis* from 2 *F. rusticolis* and 1 *F. peregrinus* for DNA sequencing of the cox1, 18S rRNA, and 28S rRNA genes. Their (2016) phylogenetic analysis showed that *E.* (= *C.*) *megafalconis* oocysts from bustards were identical with those from falcons. Sequences of *E.* (= *C.*) *neofalconis* and *E.* (= *C.*) *daceloe* (Yang et al, 2014) were situated in neighboring clades while sequences of *E.* (= *C.*) *bigenetica* (Wacha and Christiansen, 1982) from rattlesnakes were at a distinct distance. This suggested to Schuster et al. (2016) that despite structural similarities of the oocysts, there are differences between *Caryospora*-like species of birds and reptiles. This stimulated them to coin a new genus name, *Avispora*, for all bird caryosporans. This idea has not been widely accepted by scholars who work in this area.

Mateuta and Samour (2017) surveyed 3,975 fecal samples from 6 falcon species plus 2 hybrid species in the United Arab Emirates and reported 297 (7.5%) positive for oocysts of *Caryospora*-like species: 54/297 (18%) were infected with *E.* (= *C.*) *megafalconis*. Their (2017) *E.* (= *C.*) *megafalconis* oocysts measured L × W: 42.2 × 35.9 (39–49 × 30–40), sporocysts were L × W: 23.6 × 22.7 (21–27 × 20–26), and SZs were L × W: 16.5 × 4.2 (11–20 × 3–6). From the data presented by Mateuta and Samour (2017), it was not possible to determine which host species/hybrids were infected by *E.* (= *C.*) *megafalconis*, nor the prevalence of infections in those infected.

***Eumonospora* (= *C.*) *mochogalegoi* (Cardozo, Berto, Caetano, Maniero, Santos, Pereira de Fonseca and Lopes, 2017) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020**

Synonym: Avispora mochogalegoi Cardozo, Berto, Caetano, Maniero, Santos, Pereira de Fonseca and Lopes, 2017.

Type host: Athene noctua (Scopoli, 1769), little owl (Strigidae).

Other hosts: None to date.

Type locality: Portugal: Lisbon, Lisbon Center for Wild Animal Recovery (LxCRAS) (38°44′22.9″N, 9°11′02.3″W).

Sporulated oocyst: Ellipsoidal; number of walls: 2, ~1.5 thick; wall characteristics: outer layer is colorless, smooth; L × W (N = 15): 38.9 × 32.9 (37–43 × 31–37); L/W ratio: 1.2 (1.15–1.23); M, OR, PG, all absent.

Sporocyst and sporozoites: Subspheroidal; L × W (N = 15): 21.1 × 20.1 (20–24 × 19–23); L/W ratio: 1.0; SB, SSB, PSB: all absent; SR: present; SR characteristics: irregular subspheroidal body composed of numerous granules that appear to be membrane-bounded and measured L × W (N = 15): 13.6 × 13.1 (11–16 × 11–16); SZ: stout, sausage-shaped bodies that measured L × W (N = 5): 16.6 × 4.7 (15–18 × 4–5), each with striations at more pointed end and a round RB, ~3 wide.

Prevalence: Cardozo et al. (2017, 2019) found oocysts of this species in 12/18 (67%) fecal samples collected from little owls at the LxCRAS in Lisbon.

Sporulation: Exogenous. Oocysts became fully sporulated by day 7 when left at room temperature in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: Schuster et al. (2016) found oocysts of *E.* (= *C.*) *megafalconis* in fecal samples and large intestinal contents of 5 wild-caught *Chlamydotis macqueenii* (Gray) (MacQueen's bustard) and in 19 captive *Chl. undulata* (Jaquin) (Houbara bustard). Using these oocysts and those of *E.* (= *C.*) *neofalconis* from 2 *F. rusticolis* and 1 *F. peregrinus*, they used DNA sequencing of the cox1, 18S rRNA, and 28S rRNA to build phylogenetic trees for all 3 genes. Their results allowed them to conclude that sequences of *E.* (= *C.*) *megafalconis* from bustards and falcons were identical and that other named caryosporan species were in neighboring, sometimes distant clades. This suggested to them (2016) that despite morphological similarities of sporulated oocysts, the *Caryospora* species of reptiles and birds were genetically different. For this reason, they thought it was reasonable to transfer avian *Caryospora* species into their new genus, *Avispora*. A year later, Cardozo et al. (2017) described this species and named it *Avispora mochogalegoi*, but it seems all these authors were unaware of an earlier paper by Allen (1933), which might have helped solve their problem without having to create a new genus. Cardozo et al. (2017) noted that sporulated oocysts of *E.* (= *C.*) *bubonis* and *E.* (= *C.*) *henryae* have oocyst measurements quite similar to those of *E.* (= *C.*) *mochogalegoi* and that the only difference between these 3 morphotypes is the structure of the SR, which is disbursed in the first 2 and compact, appearing to be enclosed in a membrane, in the latter. This seems a very trivial character upon which to base the existence of a new species, in my opinion.

***Eumonospora* (= *C.*) *neofalconis* (Böer, 1982) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020**

Type host: Falco mexicanus Schlegel, 1850, prairie falcon (Falconidae). Böer did not specifically name a type host for this caryosporan. I am using the first falcon species in which he said he found this parasite as the type.

Other hosts: Falco biarmicus Temminck, 1825, lanner falcon (Falconidae); *Falco cherrug* Gray, J.E., 1834, saker falcon (Falconidae); *Falco peregrinus* Tunstall, 1771, peregrine falcon (Falconidae); *Falco rusticolus* L., 1758, gyrfalcon (Falconidae); *Falco subbuteo* L., 1758, Eurasian hobby (Falconidae); *Falco tinnunculus* L., 1758, European kestrel (Falconidae); *Falco columbarius* L., 1758, merlin (Falconidae); *Bubo scandiacus* (syn. *Nyctea scandiaca*) (L., 1758), snowy owl (Strigidae); hybrid *Falco peregrinus peregrinator* (hybrid), black shaheen (Falconidae); *Aquila chrysaetos* (L., 1758), golden eagle (Acciptridae).

Type locality: Germany.

Sporulated oocyst: Spheroidal to subspheroidal (photomicrographs); number of walls: not stated; wall characteristics: smooth, colorless; L × W: 27.0 × 23.8 (23–32 × 20–29); L/W ratio: 1.1; M, OR, PG: all absent.

Sporocyst and sporozoites: Ovoidal; L × W: 18.8 × 14.8 (16.5–22 × 14–16); L/W ratio: 1.3; SB, SSB, PSB: all absent; SR: present; SR characteristics: described only as a granular residual body; SZ: not described or pictured.

Prevalence: Böer (1982) examined fecal material of 628 birds of prey representing 18 species (Falconiformes) and found 75/628 (12%) to be discharging oocysts of a *Caryospora*-like morphotype (56/628, 9%) or sporocysts of an *Isospora* species (19/628, 3%). He identified the caryosporan as a new species, named it *E.* (= *C.*) *neofalconis*, and said he found it in 1 prairie falcon (*F. mexicaus*),1 European hobby (*F. subbuteo*), 1 lanner falcon (*F. biarmicus*), and 9 peregrine falcons (*F. peregrinus*). Forbes and Simpson (1997) found *E.* (= *C.*) *neofalconis* in 16/16 merlins and in the only snowy owl they examined during their survey of *Caryospora*-like species as an emerging threat to captive-bred raptors in the UK. Volf and Modrý (1998) reported on their survey of fecal samples of 397 birds of prey from raptor rehabilitation centers, zoos, and private raptor keepers in the Czech Republic; they found oocysts of *E.* (= *C.*)

neofalconis in 1/47 (2%) *F. cherrug,* in 4/26 (15%) *F. peregrinus*, in 3/47 (6%) *F. tinnunculus*, and in 1/10 (10%) *A. chrysaetos*, but they provided no measurements or other data. Santana-Sánchez et al. (2015) examined the feces of 60 raptors (Falconiformes) from 3 states in central Mexico; only 1/26 (4%) *F. peregrinus* was found to be passing oocysts of a *Caryospora* sp. that they identified as *E.* (= *C.*) *neofalconis* when sporulated oocysts were measured and a sequence for the 18S rRNA gene was analyzed phylogenetically; their (2015) analysis showed a close relationship (99.2% similarity) to an Australian caryosporan, *E.* (= *C.*) *daceloe*.

Sporulation: Exogenous. Böer (1982) said sporulation was completed in 3–4 days at 21°C.

Remarks: Böer (1982) determined the prepatent period for *E.* (= *C.*) *neofalconis* experimentally in 1 *F. subbuteo* and in 7 *F. tinnunculus* to be 8–10 days, and patency lasted 2–13 weeks. He (1982) also did some cross-transmission studies and was able to transfer this parasite to *F. subbuteo* and *F. tinnunculus*, but not to the common buzzard (*Buteo buteo* [L., 1758]), Eurasian goshawk (*Accipiter gentilis* [L., 1758]), European sparrowhawk (*A. nisus* [L., 1758]), red kite (*Milvus milvus* [L., 1758]), Eurasian eagle owl (*Bubo bubo* [L., 1758]), or to the long-eared owl (*Asio otus* [L., 1758]).

Klüh (1994) experimentally infected hawks with 1,000 oocysts each of *E.* (= *C.*) *megafalconis, E.* (= *C.*) *kutzeri,* and *E.* (= *C.*) *neofalconis* and determined that the prepatent time differed for each species: ~219 hours for *E.* (= *C.*) *megafalconis,* ~264 hours for *E.* (= *C.*) *kutzeri,* and ~271 hours for *E.* (= *C.*) *neofalconis*.

Forbes and Simpson's (1997) case study of juvenile merlins (*F. columbarius*) and a juvenile snowy owl (*B. scandiacus*) (above) in the U.K. showed that infected and affected birds exhibited clinical signs of regurgitation, depression, reduced appetite, hemorrhagic feces, diarrhea, weight loss, or acute death. Results of histologic examination in 5 other merlins at necropsy revealed hemorrhagic foci in the small intestines caused by *E.* (= *C.*) *neofalconis*.

Pavlík et al. (1998) examined 91 birds of prey, representing 10 species, from the Falcon Breeding Facility in Milotíce, Czech Republic, and collected 430 fecal samples from them. They reported oocysts of *E.* (= *C.*) *neofalconis* and clinical signs (diarrhea, reduced food intake) in the following birds: in 7/25 (28%) *F. peregrinus* (peregrine falcon) and 3/7 (43%) infected birds showed clinical signs; in 14/39 (36%) *F. cherrug* (saker falcon) and 2/14 (14%) infected birds showed clinical signs; in 7/12 (58%) hybrids (*F. peregrinus* × *F. cherrug*) and 2/7 (28.5%) infected birds showed clinical signs; in 1/4 (25%) *A. gentilis* (goshawk) which showed no clinical signs; and in 1/1 (100%) *A. nisus* (sparrowhawk) which showed no clinical signs.

Santana-Sánchez et al. (2015) said they found this species in 1 peregrine falcon in central Mexico, and theirs was the first report of this species from Mexico and from the Americas. The oocysts they measured were spheroidal to subspheroidal, L × W: 26.3 × 23.9, with sporocysts that measured L × W (N = 30): 17.9 × 14.8.

Mateuta and Samour (2017) surveyed 3,975 fecal samples from 6 falcon species plus 2 hybrid species in the United Arab Emirates and reported 297 (7.5%) positive for oocysts of *Caryospora* species; 76/297 (25.5%) were infected with *E.* (= *C.*) *neofalconis*. Their (2017) *E.* (= *C.) neofalconis* oocysts measured L × W: 25.6 × 22.5 (20–30 × 19–28), sporocysts were L × W: 17.2 × 15.2 (13–19 × 12–19), and SZs were L × W: 9.9 × 2.4 (8–12 × 2–4). From the data presented by Mateuta and Samour (2017), it was not possible to determine which host species/hybrids were infected by *E.* (= *C.*) *neofalconis*, nor the prevalence of infections in those infected.

***Eumonospora* (= *C.*) *peneireiroi* (Cardozo, Berto, Caetano, Maniero, Pereira de Fonseca, and Lopes, 2016) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020**

Type host: Falco tinnunculus L., 1758, common kestrel (Falconidae).

Other hosts: None to date.

Type locality: Portugal: Lisbon, Monsanto Forest Park, Lisbon Center for Wild Animal Recovery (38°44′22.9″N, 9°11′02.3″W).

Sporulated oocyst: Ellipsoidal; number of walls: 2, ~2 thick; wall characteristics: smooth, colorless; L × W (N = 20): 47.1 × 37.6 (42–49 × 34–40); L/W ratio: 1.25 (1.2–1.4); M, OR, PG: all absent.

Sporocyst and sporozoites: Subspheroidal, sometimes appears slightly wrinkled; L × W (N = 20): 25.1 × 24.3 (24–27 × 24–25); L/W ratio: 1.0 (1.0–1.1); SB, SSB, PSB: all absent; SR: present; SR characteristics: composed of many homogeneous globules scattered throughout periphery of the sporocyst; SZ: sausage-shaped (line drawing and photomicrographs), L × W (N = 5): 17.0 × 4.2 (15–18 × 3–5), without striations but with a spheroidal posterior RB that was 3.0 (2–4) wide and a single N in the mid-body.

Prevalence: Cardozo et al. (2016, 2019) found this species in 5/27 (19%) fecal samples housed in the Lisbon Center for Wild Animal Recovery.

Sporulation: Exogenous. Oocysts became fully sporulated by day 7 in 2.5% (w/v) potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: Cardozo et al. (2016) compared the sporulated oocysts they recovered from kestrels to *Caryospora* species, with similar sized oocysts and sporocysts, that

previously had been described from predatory birds in 2 closely related bird orders, Accipitriformes (Accipitridae) and Falconiformes (Falconidae). Three caryosporan species in the Accipitridae, *E.* (= *C.*) *aquilae* Volf et al. (2000), *E.* (= *C.*) *petersoni* McAllister et al. (2013a), and *E.* (= *C.*) *hanebrinki* McAllister et al. (2013b). The argument they made to distinguish their form from the others was based on reasonably trivial differences in the surface of the sporocyst wall (wrinkled vs. smooth), the size of SZ and whether they had striations or not, and the composition of the SR. They (2016) also compared their oocysts to 2 caryosporan species from members of the Falconidae, *E.* (= *C.*) *megafalconis* (Klüh, 1994) and *E.* (= *C.*) *biarmicusis* (Alyousif et al., 2011), once again using rather trivial distinctions of the surface of the SP and the structure of the SR.

***Eumonospora* (= *C.*) *petersoni* (McAllister, Duszynski and McKown, 2013b) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020**

Type host: Accipiter striatus Vieillot, 1808, sharp–shinned hawk (Accipitridae).

Other hosts: None to date.

Type locality: USA: Kansas, Riley County, Manhattan, 2308 Cheryl Terrace (39.208759ºN, 96.615247ºW).

Sporulated oocyst: Subspheroidal; number of walls: 2, ~2.2 thick; wall characteristics: outer is smooth, ~1.6 thick, inner ~0.6 thick; L × W (N = 17): 43.1 × 39.8 (38–46 × 37–42); L/W ratio: 1.1 (1.0–1.1); M, OR, PG: all absent.

Sporocyst and sporozoites: Spheroidal to subspheroidal; L × W (N = 17): 23.4 × 23.3 (21–26 × 21–26); L/W ratio: 1.05 (1.0–1.1); SB, SSB, PSB: all absent; SR: present; SR characteristics: composed of a spheroidal mass of granules, ~15.1 (10–18) thick; SZ: stout, sausage-shaped (line drawing and photomicrographs), L × W (N = 10): 15.6 × 4.2 (15–16 × 4–5), with vertical striations, and 1 spheroidal RB ~3.0 (2–4) wide and a single N in midbody.

Prevalence: McAllister et al. (2013b) found this species in the only fecal sample of *A. striatus* they had to examine.

Sporulation: Exogenous. Unsporulated oocysts from the feces became fully sporulated by day 4 in 2.5% (w/v) potassium dichromate ($K_2Cr_2O_7$) solution at room temperature.

Remarks: McAllister et al. (2013b) compared the sporulated oocysts of this species only to oocysts previously described from members of the Accipteridae because members of this family comprise a fairly closely related group of birds (hawks, kites, eagles) that may be a distinct monophyletic lineage and the few cross-transmission studies that have been done (e.g., Böer, 1982) were unable to tramsmit caryosporans from falconids to accipters. McAllister et al. (2013b) admitted that the sporulated oocysts of *E.* (= *C.*) *petersoni* and those of *E.* (= *C.*) *aquilae* from the golden eagle (*A. chrysaetos*) in the Czech Republic are nearly identical in most qualitative and quantitative analytics. Their argument for differentiating the 2 forms is based on minor structural differences, subtle striations in the SZs, configuration of the SRs, and their host genera are currently placed in different, somewhat distant subfamilies in the Accipiteridae. Whether or not these differences are real and significant needs to be confirmed between these species via gene sequencing and phylogenetic analysis.

***Eumonospora* (= *C.*) *strigis* (Gottschalk, 1972) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020**

Type host: Tyto alba (Scopoli, 1769), barn owl (Tytonidae).

Other hosts: None to date.

Type locality: Germany: Thuringia.

Sporulated oocyst: Ovoidal; number of walls: 1 (line drawing); wall characteristics: smooth; L × W: 13.8 × 10.9 (12–15 × 10–12.5); L/W ratio: 1.3; M, OR, PG: all absent.

Sporocyst and sporozoites: Sporocyst wall thin, usually disintegrating such that SR and SZ are free within the oocyst; SB, SSB: apparently both absent, as neither was pictured or mentioned; SZ: 7.5 × 3.4.

Prevalence: Unknown.

Sporulation: Exogenous. Sporulation occurred in 72–96 hours at room temperature in 2.0% ($K_2Cr_2O_7$) solution.

Remarks: The description of this "species" is woefully inadequate by every measure, with virtually no information on the sporocyst except that Gottschalk's (1972) line drawing showed there was no SB/SSB complex present. This species is another one that has not been reported again since its discovery.

***Eumonospora* (= *C.*) *tremula* (Allen, 1933) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020**

Synonym: Eumonospora tremula Allen, 1933; *Caryospora tremula* (Allen, 1933) Hoare, 1934.

Type host: Cathartes aura (L., 1758), turkey vulture (Cathartidae).

Other hosts: None to date.

Type locality: USA: Washington, D.C.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2 (line drawing); wall characteristics: very thick, smooth, pale blue; L × W: (33–35 × 28–30); L/W ratio: 1.2; M, OR, PG: all absent (Allen, 1933); or, subspheroidal to ellipsoidal to occasionally ovoidal; number of walls 2; wall characteristics: outer layer smooth, 1.0–1.4 thick and inner layer is 0.6–0.8 thick; L × W (N = 100): 33.4 × 28.0 (30–38 × 25–32); L/W ratio: 1.2 (1.1–1.5); M: absent; PG or small OR (not both) rarely present (Lindsay et al., 1994, photomicrograph, Fig. 3, p. 14).

Sporocyst and sporozoites: Spheroidal; L × W: 23.5–25 wide; SB, SSB, PSB: all absent (Allen, 1933); or, spheroidal to subspheroidal; L × W (N = 75): 20.4 × 20.1 (19–22 × 19–22); L/W ratio: 1.0; SB, SSB, PSB all absent; SR: present; SR characteristics: many scattered granules when completely sporulated; SZ: sausage-shaped (photomicrograph, Fig. 1, p. 14) and measured, L × W (N = 25): 16.3 × 5.2 (15–18 × 5–6), each SZ tapered slightly at 1 end and had an ellipsoidal to spheroidal RB at the other end (Lindsay et al., 1994).

Prevalence: Allen (1933) found this species in the only *C. aura* she examined. Lindsay et al. (1994) found it in 3/3 *C. aura* they examined, 2 from Kansas and 1 from Alabama.

Sporulation: Exogenous. Lindsay et al. (1994) found that some oocysts completed sporulation within 48 hours and that all oocysts were sporulated in 4 days in 2.5% (w/v) aqueous potassium dichromate ($K_2Cr_2O_7$) solution at room temperature (22–24°C).

Remarks: Allen (1933) created the genus *Eumonospora* to accommodate the new coccidian that she named *Eumonospora tremula*. However, Hoare (1934) quickly synonymized *Eumonospora* with *Caryospora*, which was accepted by Allen (1934). Allen (1933) tried unsuccessfully to infect 3 chickens with sporulated oocysts recovered from *C. aura*, and Lindsay et al. (1994) also were unable to achieve infection when they fed sporulated oocysts to 7 female Hsd:ICR mice and 4 female cotton rats.

Eumonospora (= *C.*) *undata* (Schwalbach, 1959) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Synonym: Caryospora undulata Poelma and Strik, 1966 (*lapsus*).

Type host: Larus argentatus Pontoppidan, 1763, European herring gull (Laridae).

Other hosts: Uria aalge aalge (Pontoppian, 1763), common murre or guillemot (Alcidae).

Type locality: Germany.

Sporulated oocyst: Spheroidal, sometimes slightly asymmetrical (line drawing, Plate 27, Fig. 8, p. 493); number of walls: 1, ~0.8–1.0 thick; wall characteristics: smooth, colorless, with the inner side called undulating in its original description (Schwalbach, 1959); L × W: 30.6 × 29.3 (27–33 × 24–32); L/W ratio: 1.0 (Schwalbach, 1959, gull) or L × W (N = 50): 32.5 × 29.2 (27–42 × 24–35); L/W ratio: 1.10 (Poelma and Strik, 1966, guillemot); M, OR: both absent; PG: small, located near but not attached to inner oocyst wall (line drawing).

Sporocyst and sporozoites: Subspheroidal; L × W: 22.5 × 22.0 (ranges not given); L/W ratio: 1.0; SB, SSB, PSB: all absent; SR: present; SR characteristics: a single large globule with many additional granules; SZ: crescent or banana-shaped, ~12.3 × 3.5, each with 2 RBs.

Prevalence: Schwalbach (1959) reported in his first table (p. 437) that 31/122 (25%) *L. argentatus* examined were infected with coccidia, but it was uncertain how many of the infected birds had oocysts of *E.* (= *C.*) *undata* in their feces. Poelma and Strik (1966) found what they identified as oocysts of *E.* (= *C.*) *undata* in the feces of the only guillemot they examined, a bird in poor condition that had died while housed in the Rotterdam Zoo.

Sporulation: Exogenous. Sporulation occurred within 30 hours at 16°C in 2.5% potassium dichromate ($K_2Cr_2O_7$) solution.

Remarks: In his monographic survey of birds in Germany, Schwalbach (1959) examined the feces of 430 birds representing about 45 species, and from these samples he described 16 new coccidian species, including 3 *Eimeria* species, 11 *Isospora* species and 2 *Caryospora* species that included *E.* (= *C.*) *argentati* and *E.* (= *C.*) *undata*. Since 1959, I can find only 1 other reference to *C. undulata*, the note by Poelma and Strik (1966) that added some mensural data on sporocysts and 2 photomicrographs of oocysts; their discovery, however, was found in a family of birds (Alcidae) not closely related to herring gulls, so their interpretation may be questionable.

Eumonospora (= *C.*) *uptoni* (Lindsay and Blagburn, 1986) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020

Type host: Buteo jamaicensis borealis, (Gemlin, 1788), eastern red-tailed hawk (Accipitridae).

Other hosts: None to date.

Type locality: USA: Alabama, Auburn, Auburn University Raptor Rehabilitation Center; both infected hawks were caught in a location in southeastern Alabama.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 2, ~1.5 thick; wall characteristics: outer layer smooth, yellowish, inner layer is brownish; L × W (N = 50): 28.1 × 26.4 (25.5–31.5 × 24–28.5); L/W ratio: 1.15 (1.0–1.2); M, OR, PG, all absent, but small granular particles were sometimes observed lying adjacent to inner oocyst wall.

Sporocyst and sporozoites: Spheroidal; L × W (N = 50): 18.2 × 17.9 (18–19.5 × 16.5–18); L/W ratio: 1.0 (1.0–1.1); SB, SSB, PSB: all absent; SR: present; SR characteristics: spheroidal, L × W: 10.5 × 9.9 (9–12 × 9–10.5), eccentrically located in sporocyst, composed of numerous small granules, but sometimes these granules are disbursed throughout sporocyst; SZ: sausage-shaped (line drawing and photomicrographs), L × W (N = 50): 12.6 × 4.2 (10.5–15 × 3–4.5), without striations or visible RBs, but with a spheroidal single N in the mid-body (line drawing).

Prevalence: This species was found in 2/3 (67%) of the hawks examined. Upton, Campbell, et al. (1990) also found this species in 1/8 (12.5%) of *Buteo jamaicensis* in their study.

Sporulation: Exogenous. After 48 hours in 2.5% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution, 94/100 (94%) were fully sporulated.

Remarks: Lindsay and Blagburn (1986, 1989) compared all the oocyst, sporocyst, and SZ parameters of *E.* (= *C.*) *uptoni* to those of the 8 other caryosporan species known at that time and concluded there were sufficient differences between them to name this species as new. They also noted that during their daily fecal collections, one hawk passed oocysts for 14 days and the other hawk for only 5 days. Finally, they also said that 1 hawk had eaten a feral mouse 8 days prior to their detecting oocysts in its feces and, therefore, it was possible that the mouse was infected with *E.* (= *C.*) *uptoni*. The second hawk passed oocysts in its feces 17 days into their study, and they said it was probably infected with fecal oocysts passed by the original hawk that was infected with *E.* (= *C.*) *uptoni*.

Eumonospora *species in mammals (1)*

***Eumonospora* (= *C.*) *microti* (Saxe, Levine and Ivens, 1960) Chou, Tokiwa, Hadano, Izawa, Ueda, Kojima and Ike, 2020**

Synonyms: Caryospora sp. Saxe, 1952; *Caryospora microti* Saxe, Levine and Ivens, 1960.

Type host: Microtus pennsylvanicus (Ord, 1815), meadow vole (Cricetidae).

Other hosts: None to date.

Type locality: USA: Pennsylvania, Bucks County, Warrington Township.

Sporulated oocyst: Spheroidal to subspheroidal; number of walls: 1; wall characteristics: not described but pictured as smooth (Saxe et al., 1960, Figs. 4, 5, p. 62); L × W (N = 12): 9.8 × 9.1 (9–10.5 × 8.5–10); L/W ratio: 1.1 (1.0–1.2); M, OR, PG: all absent.

Sporocyst and sporozoites: Spheroidal to subspheroidal; L × W (N = 12): 7.3 × 6.5 (7–8.5 × 6–7); L/W ratio: 1.1 (1.0–1.4); SB, SSB, PSB: all absent; SR: present; SR characteristics: a compact mass of granules/globules surrounded by SZs (line drawings); SZ: stout, sausage-shaped bodies (line drawings).

Prevalence: Found in the only *M. pennsylvanicus* captured by Saxe (1952).

Sporulation: Exogenous. Saxe et al. (1960) said that sporulation took 10 days or more when their fecal/oocyst suspension was kept at 24–27°C in 2% chromic acid.

Remarks: Oocysts were found in the cecal contents of the 1 mouse caught by Saxe in October 1948 (Saxe, 1952). *Caryospora microti* is the only member of the genus (now *Eumonospora*) reported so far from mammals. Given this, Saxe et al. (1960) posed 2 questions that certainly merit further inquiry. First, 1 abnormal oocyst with 2 irregular protoplasmic masses was seen; this raised the question as to whether the oocyst they described as *E.* (*C.*) *microti* might not actually be abnormal oocysts of *Isospora mcdowelli*, also found in the same sample and which they also described as new. The second question that might be asked is whether *E.* (*C.*) *microti* might be a spurious parasite passing through the gut of the only vole they examined.

Eumonospora Species Inquirendae—*Birds (4)*

***Eumonospora* sp. of Cringoli, Quesada and Papparella, 1991 n. comb.**

Synonym: Caryospora sp. Cringoli, Quesada and Papparella, 1991.

Original host: Falco tinnunculus L., 1758, common or European kestrel (Falconidae).

Remarks: Cringoli et al. (1991) isolated oocysts of a *Caryospora* sp. from the feces of 2 kestrels in Italy. Oocysts were described as subspheroidal to subovoidal; oocyst wall with 2 layers and a smooth outer wall (line drawing); L × W: 41.7 × 37.1 (39–44 × 36–39); L/W ratio: 1.1; M, OR, PG: all absent. Sporocysts were spheroidal; L × W: 27.8 × 20.8 (25.5–29 × 21–24); L/W ratio: 1.3; SB, SSB, PSB: all absent; SR: present; SR characteristics: dispersed small granules; SZ: sausage-shaped (line drawing and photomicrograph), L × W: 13.9 × 5.8 (13–15 × 5–7), without striations with 1 spheroidal RB in the mid-body. Cringoli et al. (1991) compared the mensural and physical characteristics of their oocysts to the sporulated oocysts of 15 other caryosporans from birds of prey (their Table 1, pp. 43–45), and in each comparison they mentioned very slight differences that they felt separated their form from the others. However, they never attempted to give their form a binomial, new or otherwise. This form was recorded from 2 animals in 1 locality at 1 point in time and has not been found again since its initial discovery.

***Eumonospora* sp. of Montali, Rose, Smith and O'Donoghue, 2005 n. comb.**

Synonym: Caryospora sp. of Montali, Rose, Smith and O'Donoghue, 2005.

Original host: Podargus strigoides (Latham, 1801), tawny frogmouth (Podargidae).

Remarks: Montali et al. (2005, never published as a juried article) measured caryosporan oocysts from a tawny frogmouth they reported to be suffering severe coccidial disease; their oocysts were spheroidal to subspheroidal and measured L × W: 28–34 × 28–32, with ovoidal sporocysts L × W: 19–24 × 18–23. Other than size discrepancies, the main morphological difference between their oocysts and

those of Yang et al. (2014) was the presence of the large spheroidal RB in the SZ of *E.* (= *C.*) *daceloe*, not reported by Montali et al. (2005); this convinced Yang et al. (2014) that their form was a different species than the one seen by Montali et al. (2005), which the latter authors did not name. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

***Eumonospora* sp. 1 of Volf and Modrý, 1998 n. comb.**
Synonym: Caryospora sp. 1 of Volf and Modrý, 1998.

Original host: Circus aeruginosus (L., 1758), western marsh harrier (Accipiteridae).

Remarks: Volf and Modrý (1998) reported on their survey of fecal samples of 397 birds of prey from raptor rehabilitation centers, zoos, and private raptor keepers in the Czech Republic; they found oocysts of a *Caryospora* sp. #1 in 1/13 (8%) *C. aeruginosus*. Oocysts were widely ovoidal with a thick wall and measured L × W: 24.5 × 21.8 (23–25 × 21–24); M, OR, PG: all absent. Spheroidal to subspheroidal sporocysts were L × W: 16.2 × 15.6 (15–17 × 15–17); SB, SSB, PSB: all absent. No line drawings or photographs were presented in this abstract, and their conclusion was that this form's status should be an object of future study. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

***Eumonospora* sp. 2 of Volf and Modrý, 1998 n. comb.**
Synonym: Caryospora sp. 2 of Volf and Modrý, 1998.

Original host: Aquila chrysaetos (L., 1758), golden eagle (Accipitridae).

Remarks: Volf and Modrý (1998) reported on their survey of fecal samples of 397 birds of prey from raptor rehabilitation centers, zoos, and private raptor keepers in the Czech Republic; they found oocysts of *Caryospora* sp. #2 in 1/10 (10%) *A. chrysaetos* examined. Oocysts recovered were subspheroidal with a 2.2 thick wall and measured L × W: 43.0 × 37.5 (40–49 × 34–39); M, OR, PG: all absent. Spheroidal to subspheroidal sporocysts were L × W: 23.8 × 23.3 (23–25 × 22–15); SB, SSB, PSB: all absent. No line drawings or photographs were presented in their abstract, but their conclusion was that sporulated oocysts of this form were almost identical to those of *E.* (*C.*) *megafalconis* and was another form that was worthy of future study, especially because *E.* (*C.*) *megafalconis* was found in the Falconidae, not in the Accipteridae. Unfortunately, this form was recorded from 1 animal in 1 locality at 1 point in time and has not been found again since its initial discovery.

Discussion

Léger (1904) was probably the first to discover coccidian oocysts in the gut of a European asp, *Viper aspis* (L., 1758), which differed from previously known coccidians because they contained only a single sporocyst with 8 sporozoites. Later, he (Léger, 1911) suggested the name *Caryospora*. Since then, about 112 oocysts with these precise characters, 1 sporocyst + 8 SZ, have been mentioned or described in the parasite literature with a variety of monikers. These include 62 presumably valid *Caryospora* species from birds (1), lizards (4), snakes (56), and turtles (1) and 26 *Eumonospora* species from birds (25) and mammals (1). An additional 24 forms (1 sporocyst + 8 SZ) have been mentioned in the literature, but most of these are without sufficient qualitative or quantitative data, leaving their identification doubtful and without an assigned binomial name by their authors; these all had to be relegated, for the moment, to *species inquirendae*, a term that denotes their doubtful identity needing further investigation (Tables 1, 2, 3).

Apicomplexans in these 2 groups, *Caryospora* (Eimeriidae) and *Eumonospora* (Sarcocystidae), seem most often to be asymptomatic in their primary natural hosts under noncaptive conditions. However, a few species—under particular circumstances—can cause a variety of disease manifestations and even death in their host. For example, 1 or more *Caryospora*-like organisms can cause disseminated coccidiosis in dogs (Marcone, 1908; Dubey et al., 1990). These as yet unnamed species manifest as serohaemorrhagic nodules in the skin of dogs. The dermis becomes edematous and infiltrated with macrophages, plasma cells, and polymorphonuclear cells. Eosinophils become abundant in infected areas, resulting in inflammation that may extend to the subcutis and even to the subcutaneous muscles. Symptoms include anorexia, lethargy, and ocular and nasal discharge.

Another species we don't hear or know much about is the green turtle pathogen *C. cheloniae*, which causes disease and mortality in young turtles about 30 days after hatching in mariculture facilities, mostly by tissue destruction in the hindgut. This is the first, and still only, serious coccidian pathogen reported from turtles. It is an economically important pathogen of mariculture-reared green sea turtles (Leibovitz, et al., 1978) because the epidemics caused by *C. cheloniae* are unprecedented in the history of marine mariculture (Rebell et al., 1974).

Several other *Caryospora* coccidians stand out in their ability to cause symptoms of disease in their hosts. Infection by *C. duszynskii* is known to cause anorexia in some of the snake species it is capable of infecting. In snake caryosporans with known heteroxenous life histories, severe

disease and death can occur in the rats and mice that become paratenic or intermediate hosts after ingesting or being inoculated with oocysts of *C. bigenetica* or *C. simplex* (Upton, Current, Ernst, et al., 1984; Lindsay, Sundermann and Blagburn, 1988; Upton and Barnard, 1988).

Only a few *Eumonospora* species seem to be pathogenic, namely *E.* (*C.*) *kutzeri* and *E.* (*C.*) *neofalconis*, in their ability to cause severe coccidiosis in some falcon species (e.g., *F. peregrinus*, *F. cherrug*), in which infected birds exhibited clinical signs of regurgitation, depression, reduced appetite, hemorrhagic foci in the small intestines, diarrhea, weight loss, or acute death. What little information we have to date on the different *Eumonospora* species and the potential pathology they may cause raises many questions that should be answered. Can different *Eumonospora* species be transmitted between different falcon species? Do different falcon species react differently to infection with the same *Eumonospora* species? What is the difference between innate, primary, and secondary immunity of falcons to these infections? How do these immune mechanisms function in birds of prey in response to these parasites? Why is coccidiosis seldom seen in adult birds, which seem to maintain latent infections and rarely become ill? Why does the disease most often occur in nestlings and young falcons and if left untreated can lead to death (Halliwell, 1979; Keymer, 1972, Klüh, 1994)?

At least 29/62 (47%) *Caryospora* species considered currently as valid species have been found in only 1 host animal in 1 locality at 1 point in time, and some/many of these species descriptions are truly marginal in their value; these include *C. barnardae*, *C. bothriechis*, *C. brygooi*, *C. ceadsensis, C. carajasensis* (?), *C. choctawensis, C. cobrae, C. coniophanis, C. constanciae* (?), *C. epicrati* (?), *C. gekkonis, C. guatemalensis, C. heterodermus*, *C. jiroveci*, *C. kalimantanensis*, *C. maculatus, C. matatu, C. mayorum*, *C. micruri, C. minuta, C. najadae, C. natchitochesensis*, *C. olfersii, C. paraensis* (?), *C. peruensi, C. pseustesi* (?), *C. sargentae, C. telescopis,* and *C. veselyi*. Similarly, at least 6/26 (23%) *Eumonospora* currently listed as valid species also have been documented in only 1 host animal in 1 locality at 1 point in time, including *E. gloriae*, *E. hanebrinki, E. lindsayi*, *E. petersoni*, *E. strigis,* and *E. microti*. Finally, of the 28 *Caryospora* and *Eumonospora* species relegated to *species inquirendae* in this work, 12/24 (50%) *Caryospora* and 4/4 (100%) *Eumonospora* morphotypes (see text) were found only once in 1–2 animals from 1 location. Clearly, lots of work needs to be done to validate and learn more about the biology of any and all of these forms.

Some authors (Allen, 1933; Böer, 1982; Cawthorn and Stockdale, 1982) who did experimental cross-transmission studies were unable to transmit some *Eumonospora* species between multiple avian species, while others (Yakimoff and Matikaschwili, 1932; Wetzel and Enigk, 1937; Klüh, 1994; Schuster et al., 2016; Chou et al., 2020) have either been successful or have indicated that some *Eumonospora* spp. may display a wide host spectrum. Such cross transmission studies help us better understand host specificity in the life history of these apicomplexans by transferring sporulated oocysts (usually *per os*) from host to host within similar host cohorts (e.g., snake to snake). Some of these studies with *Caryospora* or *Eumonospora* species between congeneric hosts have been successful (Léger, 1911; Boer, 1982; Klüh, 1994). For example, Klüh (1994) experimentally infected hawks with 1,000 oocysts each of *E. megafalconis, E. kutzeri,* and *E. neofalconis* and determined that the prepatent time differed for each species. However, most cross-transmission attempts beyond the genus level in birds of prey have failed (Allen, 1933; Pellérdy, 1974; Cawthorn and Stockdale, 1982). Thus, eumonosporans infecting birds of prey seem to be relatively host specific at the host genus level, but exceptions exist. For example, *E. megafalconis* was found to occur in systematically distant hosts. The only other species of the genus that was found in a distant host species was *E.* (= *C.*) *undulata* described from the herring gull, *L. argentatus,* and later was diagnosed in tufted puffins, *Fratercula cirrhata*, by Upton, Odell and Walsh (1992)

Several caryosporans, *C. duszynskii, C. bigenetica*, and *C. simplex*, have viperid snakes as their primary hosts and use rodents as secondary hosts in their life cycles (Stockdale and Cawthorn, 1981; Cawthorn and Stockdale, 1982; Wacha and Christiansen, 1982; Upton, Current, Ernst, and Barnard, 1984). *Eumonospora bubonis* of the great horned owl, *B. virginianus*, also is transmissible to mice (Stockdale and Cawthorn, 1981; Cawthorn and Stockdale, 1982). However, most other species are not (yet) known to have secondary hosts (Lindsay and Sundermann, 1989; Upton, Campbell, et al., 1990; Upton and Sundermann, 1990; Lindsay et al. 1994).

Other observations emerged while compiling the data for this review. At least 10/62 (16%) *Caryospora* species (*C. ahaetullae*, *C. brygooi*, *C. choctawensis*, *C. jararacae*, *C. maculatus*, *C. madagascariensis*, *C. masticophis*, *C. matatu*, *C. minuta*, *C. serpentis*) and 9/26 (35%) *Eumonospora* species (*E. arcayae*, *E. biarmicusis*, *E. cherrughi*, *E. circi*, *E. hanebrinki*, *E. kansasensis*, *E. lindsayi*, *E. mochogalegoi*, *E. petersoni*) were noted in their original species descriptions to have various kinds of vertical or other striations on the SZs within their sporulated oocysts. This seems like a high percentage of observations describing structural features on SZs that no one seems to know anything about or has yet investigated to determine their ultrastructure and/or function(s).

Table 1. Alphabetical list of named (binomial) *Caryospora* (62) and *Eumonospora* (26) species, the hosts in which they were found, and the *species inquirendae* (28) in these genera without enough information to apply valid binomials

***Caryospora ahaetullae* Modrý & Koudela, 1994**
- *Ahaetulla nasuta* (Lacépède, 1789), long-nosed vine snake (Colubridae)
- *Ahaetulla prasina* (Boie, 1827), Gunther's or oriental whipsnake (Colubridae)

***Caryospora barnardae* Upton, Freed, et al., 1990**
- *Liopholidophis stumpffi* (Boettger, 1881), Malagasy colubrid (Colubridae)

***Caryospora bengalensis* Mandal, 1976**
- *Enhydris enhydris* Schneider, 1799, rainbow or striped water snake (Colubridae)

***Caryospora bigenetica* Wacha & Christiansen, 1982**
- *Agkistrodon contortrix* L., 1766, copperhead (Viperidae)
- *Crotalus adamanteus* Palisot de Beauvois, 1799, eastern diamondback rattlesnake (Viperidae)
- *Crotalus atrox* Baird & Giraud, 1853, western diamondback rattlesnake (Viperidae)
- *Crotalus horridus* L. 1758, timber or cane-brake rattlesnake (Viperidae)
- *Sistrurus catenaus* (Rafinesque, 1818), massasauga (natural and experimental) (Viperidae)
- *Sistrurus miliaris* L., 1766, pigmy rattlesnake (Viperidae)

***Caryospora bothriechis* Seville et al., 2005**
- *Bothriechis aurifer* Salvin, 1860, yellow-blotched palm pit viper (Viperidae)

***Caryospora brasiliensis* Carini, 1932**
- *Erythrolamprus poecilogyrus* (Weid-Neuwied, 1824), cobra verde (Colubridae)
- *Leimadophis poecilogyrus schotti* (Schlegel, 1837), cobra-corredeira (Colubridae)
- *Philodryas aestivus* (Duméril, Bibron & Duméril, 1854) (syn. *Dryophylax aestivus* Duméril, Bibron & Duméril, 1854), Brazilian or common green racer (Colubridae)
- *Philodryas nattereri* (Steindachner, 1870), Paraguay green racer (Colubridae)
- *Philodryas olfersii* (Lichtenstein, 1823), Lichtenstein's green racer (Colubridae)

***Caryospora brygooi* Upton, Freed, et al., 1990**
- *Madagascarophis colubrinus* (Schlegel, 1837), Madagascar cat-eye snake (Pseudoxyrhophiidae)

***Caryospora carajasensis* Lainson et al., 1991**
- *Oxyrhopus petola digitalis* (Reuss, 1834), forest flame snake (Colubridae)

***Caryospora ceadsensis* Tobias de Santana Miglionico & Viana, 2017**
- *Siphlophis pulcher* (Raddi, 1820), Guanabara spotted night snake (Dipsadidae)

***Caryospora cheloniae* Leibovitz et al., 1978**
- *Chelonia mydas mydas* (L., 1758), green turtle (Cheloniidae)

***Caryospora choctawensis* McAllister et al., 2012**
- *Tantilla gracilis* Baird & Girard, 1853, flat-head snake (Colubridae)

***Caryospora cobrae* Nandi, 1985**
- *Naja naja* (L., 1758), common or spectacled cobra (Elapidae)

***Caryospora colubris* Matuschka, 1984b**
- *Dolichophis jugularis* (L., 1758) (syn. *Coluber jugularis* L., 1758), large whip snake (Colubridae)
- *Eirenis decemlineatus* (Duméril, Bibron et Duméril, 1854), [no English common name] (Colubridae)
- *Hemorrhois hippocrepis* (L., 1758) (syn. *Coluber hippocrepis* L., 1758), horseshoe whip snake (Colubridae)
- *Hierophis* (*Coluber*) *viridiflavus* (Lacépède, 1798), green or western whip snake (Colubridae)

***Caryospora coniophanis* Seville et al., 2005**
- *Coniophanes imperialis* (Kennicott in Baird, 1859), black-striped snake (Colubridae)

***Caryospora conophae* Seville et al., 2005**
- *Conophis imperialis* (Duméril, Bibron & Duméril, 1854), road guarder snake (Colubridae)

***Caryospora constanciae* Lainson et al., 1991**
- *Micrurus spixii spixii* Schmidt & Walker, 1943, Amazonian coral snake (Elapidae)

***Caryospora corallae* Matuschka, 1984b**
- *Corallus cainus* (L., 1758), emerald tree boa (Boidae)

***Caryospora demansiae* Cannon, 1967**
- *Demansia psammophis* (Schlegel, 1857), yellow-faced whip snake (Elapidae)

***Caryospora dendrelaphis* Cannon & Rzepczyk, 1974**
- *Dendrelaphis punctulatus* (Gray 1826), common tree snake (Colubridae)

***Caryospora durrelli* Daszak et al., 2011a, b**
- *Casarea dussumieri* (Schlegel, 1837), Round Island boa (Bolyeridae)

***Caryospora duszynskii* Upton et al., 1984a**
- *Lampropeltis calligaster* (Harlan, 1827), prairie kingsnake (Colubridae)
- *Lampropeltis holbrooki* (Stejneger, 1902), speckled kingsnake (Colubridae)
- *Lampropeltis triangulum* (Lacépède, 1789), eastern milksnake (Colubridae)

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Masticophis flagellum (Shaw, 1802), coachwhip (Colubridae)
Pantherophis emoryi (Baird et Girard, 1853), Great Plains rat snake (Colubridae)
Pantherophis guttatus (L., 1766) (syn. *Coluber guttata* L., 1766), eastern corn snake (Colubridae)
Pantherophis obsoletus (Say, 1823) (syn. *Coluber obsoletus* Say, 1823), black ratsnake (Colubridae)

***Caryospora epicrati* Lainson et al., 1991, emend. Modrý, 1998**
Epicrates cencheria (L., 1758), rainbow boa (Boidae)

***Caryospora ernsti* Upton et al., 1984b**
Anolis carolinensis Voigt, 1832, North American green anole (Anolidae)

***Caryospora gekkonis* Chakravarty & Kar, 1947**
Gecko gecko (L., 1758), Tokay gecko (Gekkonidae)

***Caryospora gracilis* Upton, McAllister, et al., 1992**
Tantilla gracilis Baird et Girard, 1853, flat-headed snake (Colubridae)

***Caryospora guatemalensis* Seville et al., 2005**
Lampropeltis triangulum (Lacépède, 1789), eastern milksnake (Colubridae)

***Caryospora hermae* Bray, 1960**
Boaedon fuliginosus (Boie, 1827), African or brown house snake (Lamprophiidae)
Psammophis phillipsii Hallowell, 1844 (syn. *P. sibilans phillipsi* Loveridge, 1840), hissing, olive, or western sand snake (Psammophiidae)
Psammophis sibilans (L., 1758), Egyptian hissing sand snake (Psammophiidae)

***Caryospora heterodermus* Upton, Freed & Freed, 1992**
Philothamnus heterodermus Hallowell, 1857, emerald or variable green snake (Colubridae)

***Caryospora japonicum* Matubayashi, 1936**
Rhabdophis tigrinus (Boie, 1826) (syns. *Natrix tigrina* [Boie, 1826]; *Natrix tigrine* Stejneger, 1907), Yamakagashi snake of Japan or tiger keelback (Colubridae)

***Caryospora jararacae* (Carini, 1939) Lainson et al., 1991**
Bothriechis lateralis Peters, 1862, coffee palm viper (Viperidae)
Bothrops atrox (L., 1758), fer-de-lance (Viperidae)
Bothrops jararaca (Wied-Neuwied, 1824), jararaca (Viperidae)

***Caryospora jiroveci* Černá, 1976**
Erithacus rubecula (L., 1758), European robin (Muscicapidae)

***Caryospora kalimantanensis* Modrý & Koudela, 1997**
Boiga dendrophila (Boie, 1827), mangrove or gold-ringed cat snake (Colubridae)

***Caryospora lampropeltis* Anderson et al., 1968**
Heterodon platirhinos Letreille, 1801, eastern hognose snake (Colubridae)
Lampropeltis calligaster (Harlan, 1827), prairie kingsnake (Colubridae)
Lampropeltis holbrooki Stejneger, 1902, speckled kingsnake (Colubridae)
Lampropeltis triangulum (Lacépède, 1789), eastern milksnake (Colubridae)

***Caryospora legeri* Hoare, 1933**
Psammophis sibilans (L., 1758), Egyptian hissing sand snake (Psammophiidae)

***Caryospora maculatus* Upton, Freed & Freed, 1992**
Causus maculatus (Hallowell, 1842), spotted night adder (Viperidae)

***Caryospora madagascariensis* Upton, Freed, et al., 1990**
Madagascaropis colubrinus (Schlegel, 1837), Madagascar cat-eye snake (Colubridae)
Mimophis mahfalensis (Grandidier, 1867), Malagasy colubrid (Colubridae)

***Caryospora masticophis* Upton et al., 1994**
Coluber constrictor priapus Dunn & Wood, 1939, southern black racer (Colubridae)
Masticophis flagellum flagellum (Shaw, 1837), eastern coachwhip (Colubridae)

***Caryospora matatu* Modrý et al., 2002**
Atheris ceratophora Werner, 1896 (syn. *Atheris ceratophorus* Werner, 1895 of Modrý et al., 2002), horned bush viper (Viperidae)

***Caryospora maxima* Modrý et al., 1999**
Echis coloratus Günther, 1878, Palestine saw-scaled viper (Viperidae)
Psammophis schokari (Forskål, 1775), Forskål's sand snake (Psammophiidae)

***Caryospora mayorum* Seville et al., 2005**
Conophis lineatus (Duméril, Bibron & Duméril, 1854), road guarder snake (Colubridae)

***Caryospora micruri* Lainson et al., 1991**
Micrurus spixii spixii Schmidt & Walker, 1943, Amazonian coral snake (Elapidae)

***Caryospora minuta* Upton, Freed, et al., 1990**
Leioheterodon madagascariensis Duméril & Bibron, 1854, Madagascar hog-nose snake (Colubridae)

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***Caryospora najadae* Matuschka, 1986a**
Platyceps najadum (Eichwald, 1831) (syn. *Coluber najadum* Schmidt, 1939), Dahl's whip snake (Colubridae)

***Caryospora najae* Matuschka, 1982**
Naja nigricollis Reinhardt, 1843, black-necked spitting cobra (Elapidae)

***Caryospora natchitochesensis* McAllister et al., 2014**
Anolis carolinensis Voigt, 1832, North American green anole (Anolidae)

***Caryospora olfersii* Viana et al., 2013**
Philodryas olfersii (Lichtenstein, 1823), Lichtenstein's green racer (Colubridae)

***Caryospora paraensis* Lainson et al., 1991**
Oxyrhopus petola digitalis (Reuss, 1834), forest flame snake (Colubridae)

***Caryospora peruensis* Upton et al., 1989**
Xenoxybelis argenteus (Daudin, 1803), striped sharp-nosed snake (syn. *Coluber argenteus* Daudin, 1803) (Colubridae)

***Caryospora psammophi* Bray, 1960**
Psammophis phillipsii Hallowell, 1844 (syn. *P. sibilans phillipsi* Loveridge, 1840), hissing, olive, or western sand snake (Psammophiidae)

***Caryospora pseustesi* Lainson et al., 1991**
Spilotes sulphureus sulphureus (Wagler, 1824) (syn. *Pseustes sulphureus sulphureus* Beebe, 1946), yellow-bellied hissing or Amazon puffing snake (Colubridae)

***Caryospora regentensis* Daszak & Ball, 2001a, b**
Dendroaspis angusticeps (Smith, 1849), green mamba (Elapidae)
Dendroaspis viridis (Hallowell, 1844), western green mamba (Elapidae)

***Caryospora relictae* Telford, 1997**
Tantilla relicta Telford, 1966, Florida crowned snake (Colubridae)

***Caryospora sargentae* McAllister et al., 2022**
Tantilla gracilis Baird & Girard, 1853, flathead snake (Colubridae)

***Caryospora saudiarabiensis* (Modrý et al., 1999) Duszynski & Upton, 2010**
Echis carinatus (Schneider, 1801), saw-scaled or African carpet viper (Viperidae)

***Caryospora serpentis* Upton, Freed, et al., 1990**
Leioheterodon madagascariensis Duméril & Bibron, 1854, Madagascar hognose snake (Colubridae)
Madagascarophis colubrinus (Schlegel, 1837), Madagascar cat-eye snake (Pseudoxyrhophiidae)
Mimophis mahfalensis (Grandidier, 1867), Malagasy colubrid (Colubridae)

***Caryospora simplex* Léger, 1911**
Daboia palestinae (Werner, 1938) (syn. *Vipera palestinae* Werner, 1938), Palestine viper (Viperidae)
Daboia russelii (Shaw & Nodder, 1797) (syn. *Vipera russellii* Strauch, 1869), Russell's viper (Viperidae)
Montivipera xanthina (Gray, 1849) (syn. *Vipera xanthina* Gray, 1849), Ottoman or coastal viper (Viperidae)
Vipera ammodytes (L., 1758), nose-horned or sand viper (Viperidae)
Vipera aspis (L., 1758), European asp or asp viper (Viperidae)
Vipera berus (L., 1758), adder or northern viper (Viperidae)
Vipera kaznakovi Nikolsky, 1909, Caucasus viper (Viperidae)

***Caryospora tantillae* Telford, 1997**
Tantilla relicta Telford, 1966, Florida crowned snake (Colubridae)

***Caryospora telescopis* Matuschka, 1986b**
Telescopus fallax (Fleischmann, 1831), European or Mediterranean cat snake (Colubridae)

***Caryospora varaniornati* Modrý et al., 2001**
Varanus (*Polydaedalus*) *ornatus* (Daudin, 1803), ornate monitor (Varanidae)

***Caryospora veselyi* Modrý & Koudela, 1998**
Ahaetulla nasuta (Lacépède 1789), long-nosed tree or whip snake (Colubridae)

***Caryospora weyerae* Bray, 1960**
Psammophis phillipsii Hallowell, 1844 (syn. *P. sibilans phillipsi* Loveridge, 1840), hissing, olive, or western sand snake (Psammophiidae)

***Caryospora zacapensis* Seville et al., 2005**
Masticophis mentovarius (Duméril et al., 1854), Neotropical whip snake (Colubridae)

***Eumonospora aquilae* (Volf et al., 2000) Chou et al., 2020**
Aquila chrysaetos (L., 1758), golden eagle (Accipitridae)

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***Eumonospora arcayae* (Volcán & Medrano, 1984) Chou et al., 2020**
Buteo magnirostris (Gmelin, J.F., 1788), roadside hawk (Accipitridae)
Buteo platypterus (Vieillot, 1823), broad-winged hawk (Accipitridae)
Rupornis magnirostris (Gmelin, J.F., 1788) (syn. *Falco magnirostris* Gmelin, J.F., 1788) (Accipitridae)

***Eumonospora argentati* (Schwalbach, 1959) Chou et al., 2020**
Larus argentatus Pontoppidan, 1763, European herring gull (Laridae)

***Eumonospora biarmicusis* (Alyousif et al., 2011) Chou et al., 2020**
Falco biarmicus Temminck, 1825, lanner falcon (Falconidae)

***Eumonospora boeri* (Klüh, 1994) Chou et al., 2020**
Falco tinnunculus L., 1758, European kestrel (Falconidae)

***Eumonospora bubonis* (Cawthorn & Stockdale, 1981) Chou et al., 2020**
Bubo bubo (L., 1758), Eurasian eagle owl (Strigidae)
Bubo virginianus (Gmelin, 1788), great horned owl (Strigidae)

***Eumonospora cherrughi* (Alfaleh et al., 2013) Chou et al., 2020**
Falco cherrug Gray, J.E., 1834, saker falcon (Falconidae)

***Eumonospora circi* (Volf et al., 2000) Chou et al., 2020**
Circus aeruginosus (L., 1758), western marsh harrier (Accipitridae)

***Eumonospora daceloe* (Yang et al., 2014) Chou et al., 2020**
Dacelo novaeguineae (Hermann, 1783), laughing kookaburra (Alcedinidae)

***Eumonospora falconis* (Wetzel & Enigk, 1937) Chou et al., 2020**
Athene noctua (Scopoli, 1769), little owl (Strigidae)
Falco peregrinus Tunstall, 1771, peregrine falcon (Falconidae)
Falco subbuteo L., 1758, Eurasian hobby (Falconidae)
Falco tinnunculus L., 1758, European kestrel (Falconidae)

***Eumonospora gloriae* (Pellérdy, 1967) n. comb.**
Ptiloxena atroviolacea (d'Orbigny, 1839) (syn. *Dives atroviolaceus*), Cuban blackbird or toti (Icteridae)

***Eumonospora hanebrinki* (McAllister et al., 2013a) Chou et al., 2020**
Haliaeetus leucocephalus (L.,1766), bald eagle (Accipitridae)

***Eumonospora henryae* (emend. Pellérdy, 1974) Chou et al., 2020**
Athene noctua (Scopoli, 1769), little owl (Strigidae)
Bubo bubo (L., 1758), Eurasian eagle-owl (Strigidae)
Bubo scandiacus (L., 1758) (syn. *Nyctea scandiaca* (L., 1758)), snowy owl (Strigidae)
Cathares aura (L., 1758), turkey vulture (Cathartidae)
Falco columbarius L., 1758, merlin (Falconidae)
Falco subbuteo L., 1758, Eurasian hobby (Falconidae)
Falco tinnunculus L., 1758, European kestrel (Falconidae)
Milvus migrans (Boddaert, 1783), black kite (Accipitridae)
Ptilosis leucotis (Temminck, 1820), northern white-faced owl (Strigidae)
Strix nebulosi Foster, 1772, great gray owl (Strigidae)

***Eumonospora kansasensis* (Upton, Campbell, et al., 1990) Chou et al., 2020**
Buteo swainsoni Bonaparte, 1838, Swainson's hawk (Accipitridae)

***Eumonospora kutzeri* (Böer, 1982) Chou et al., 2020**
Bubo scandiacus (L., 1758) (syn. *Nyctea scandiaca* (L., 1758)), snowy owl (Strigidae)
Falco biarmicus Temminck, 1825, lanner falcon (Falconidae)
Falco cherrug Gray, J.E., 1834, saker falcon (Falconidae)
Falco columbarius L., 1758, merlin (Falconidae)
Falco jugger Gray, J.E., 1834, laggar falcon (Falconidae)
Falco mexicanus Schlegel, 1850, prairie falcon (Falconidae)
Falco peregrinus Tunstall, 1771, peregrine falcon (Falconidae)
Falco rusticolus L., 1758, gyrfalcon (Falconidae)
Falco subbuteo L., 1758, Eurasian hobby (Falconidae)
Falco tinnunculus L., 1758, European kestrel (Falconidae)

***Eumonospora lindsayi* (Upton, Campbell, et al., 1990) Chou et al., 2020**
Buteo jamaicensis (Gemlin, 1788), red-tailed hawk (Accipitridae)

***Eumonospora megafalconis* (Klüh, 1994) Chou et al., 2020**
Chlamydotis macqueenii (Gray, J.E., 1832), MacQueen's bustard (Otididae)
Chlamydotis undulata (Jacquin, 1784), Houbara bustard (Otididae)
Falco cherrug Gray, J.E., 1834, saker falcon (Falconidae)
Falco peregrinus Tunstall, 1771, peregrine falcon (Falconidae)
Falco rusticolus L., 1758, gyrfalcon (Falconidae)
Falco tinnunculus L., 1758, European kestrel (experimentally) (Falconidae)
Ger-saker hybrid (Falconidae)

Table 1. Alphabetical list of named (binomial) *Caryospora* (62) and *Eumonospora* (26) species, the hosts in which they were found, and the *species inquirendae* (28) in these genera without enough information to apply valid binomials (*continued*)

***Eumonospora microti* (Saxe et al., 1960) Chou et al., 2020**
Microtus pennsylvanicus (Ord, 1815), meadow vole (Cricetidae)

***Eumonospora mochogalegoi* (Cardozo et al., 2017) Chou et al., 2020**
Athene noctua (Scopoli, 1769), little owl (Strigidae)

***Eumonospora neofalconis* (Böer, 1982) Chou et al., 2020**
Aquila chrysaetos (L., 1758), golden eagle (Accipitridae)
Bubo scandiacus (L., 1758) (syn. *Nyctea scandiaca*), snowy owl (Strigidae)
Falco biarmicus Temminck, 1825, lanner falcon (Falconidae)
Falco cherrug Gray, J.E., 1834, saker falcon (Falconidae)
Falco columbarius L., 1758, merlin (Falconidae)
Falco mexicanus Schlegel, 1850, prairie falcon (Falconidae)
Falco peregrinus Tunstall, 1771, peregrine falcon (Falconidae)
Falco peregrinus peregrinator (hybrid), black shaheen (Falconidae)
Falco rusticolus L., 1758, gyrfalcon (Falconidae)
Falco subbuteo L., 1758, Eurasian hobby (Falconidae)
Falco tinnunculus L., 1758, European kestrel (Falconidae)

***Eumonospora peneireiroi* (Cardozo et al., 2016) Chou et al., 2020**
Falco tinnunculus L., 1758, European kestrel (Falconidae)

***Eumonospora petersoni* (McAllister et al., 2013b) Chou et al., 2020**
Accipiter striatus Vieillot, 1808, sharp-shinned hawk (Accipitridae)

***Eumonospora strigis* (Gottschalk, 1972) Chou et al., 2020**
Tyto alba (Scopoli, 1769), barn owl (Tytonidae)

***Eumonospora tremula* (Allen, 1933) Chou et al., 2020**
Cathartes aura (L.,1758), turkey vulture (Cathartidae)

***Eumonospora undata* (Schwalbach, 1959) Chou et al., 2020**
Larus argentatus Pontoppidan, 1763, European herring gull (Laridae)
Uria aalge aalge (Pontoppian, 1763), common murre or guillemot (Alcidae)

***Eumonospora uptoni* (Lindsay & Blagburn, 1986) Chou et al., 2020**
Buteo jamaicensis borealis (Gemlin, 1788), eastern red-tailed hawk (Accipitridae)

Species Inquirendae (28)

***Caryospora* sp. of Daszak, 1995**
Casarea dussumieri (Schlegel, 1837), Round Island boa (Bolyeriidae)

***Caryospora* sp. of Fernandes-Grego et al., 2004**
Bothrops jararaca Weid-Neuwied, 1824, jaracara (Viperidae)

***Caryospora* sp. of Frye, 1981**
Python sp. (Pythonidae)

***Caryospora* sp. of Hoge-1 (*Bothrops* spp.), 1991**
Bothrops jararaca (Wied-Neuwied, 1824), jararaca (Viperidae)
Bothrops neuwiedi Wagler, 1824, Wied's lance-head (Viperidae)

***Caryospora* sp. of Hoge-2 (*Crotalus* sp.), 1991**
Crotalus durissus L.,1758, Cascabel rattlesnake (Viperidae)

***Caryospora* sp. of Hoge-3 (*Tomodon* sp.), 1991**
Tomodon dorsatus Duméril, Bibron et Duméril, 1854, pampas snake (Colubridae)

***Caryospora* sp. 1 of Koudela et al., 2000**
Calloselasma rhodostoma (Kuhl, 1824), Malayan pit viper (Viperidae)

***Caryospora* sp. 2 of Koudela et al., 2000**
Atheris nitschei Tornier, 1902, Nitsche's bush viper (Viperidae)

***Caryospora* sp. 3 of Koudela et al., 2000**
Vipera ursinii (Bonaparte, 1835), Ursini's viper (Viperidae)

***Caryospora* sp. 4 of Koudela et al., 2000**
Varanus niloticus (L., 1758), Nile monitor (Varanidae)

***Caryospora* sp. of Liu et al., 2020**
Grallina cyanoleuca (Latham, 1801), magpie lark (Monarchidae)

***Caryospora* spp. (in dogs) of Marcone, 1908 and others**
Canis familiaris L. 1758, domestic dog (Canidae)

***Caryospora* sp. of Matuschka, 1986b**
Vipera kaznakovi Nikolsky, 1909, Caucasus viper (Viperidae)

***Caryospora* sp. 1 of Modrý, 1998**
Atheris nitschei Tornier, 1902, Niche's bush viper (Viperidae)

Table 1. Alphabetical list of named (binomial) *Caryospora* (62) and *Eumonospora* (26) species, the hosts in which they were found, and the *species inquirendae* (28) in these genera without enough information to apply valid binomials (*continued*)

***Caryospora* sp. 2 of Modrý, 1998**
Calloselasma rhodostoma (Kuho, 1824), Malayan pit viper (Viperidae)

***Caryospora* sp. I of Šlapeta et al., 2003**
Psammophis orientalis Broadley, 1977, eastern stripe-bellied sand snake (Colubridae)

***Caryospora* sp. II of Šlapeta et al., 2003**
Psammophis orientalis Broadley, 1977, eastern stripe-bellied sand snake (Colubridae)

***Caryospora* sp. of Upton & Sundermann, 1990**
Bothriechis lateralis Peters, 1862, coffee-palm viper (Viperidae)

***Caryospora* sp. of Varghese & Yayabu, 1981**
Diphyllodes magnificus (Pennant, 1781), magnificent bird-of-paradise (Paradisaeidae)

***Caryospora* sp. of Wetzel & Enigk, 1939**
Athene noctua (Scopoli, 1769), little owl (Strigidae)

***Caryospora* sp. of Yakimoff & Matschulsky, 1936 (ovoidal form, in part, 1936)**
Milvus migrans (Boddaert, 1783), black kite (Accipitridae)

***Caryospora* sp. of Yakimoff & Matschulsky, 1936 (round form, in part, 1936)**
Milvus migrans (Boddaert,1783), black kite (Accipitridae)

***Caryospora varani* of Kaur & Oberoi, 1987**
Varanus sp. Merrem, 1820, carnivorous lizard (Varanidae)

***Caryospora zuckermanae* of Bray, 1960**
Hemorrhois ravergieri Ménétries, 1832 (syn. *Coluber ravergieri nummifer* Reuss, 1843), spotted whip snake (Colubridae)

***Eumonospora* sp. of Cringoli et al., 1991 n. comb.**
Falco tinnunculus L., 1758, common or European kestrel (Falconidae)

***Eumonospora* sp. of Montali et al., 2005 n. comb.**
Podargus strigoides (Latham, 1801), tawny frogmouth (Podargidae)

***Eumonospora* sp. 1 of Volf & Modrý, 1998 n. comb.**
Circus aeruginosus (L., 1758), western marsh harrier (Accipiteridae)

***Eumonosporaa* sp. 2 of Volf & Modrý, 1998 n. comb.**
Aquila chrysaetos (L., 1758), golden eagle (Accipiteridae)

Table 2. Alphabetical list of all vertebrate host species documented to have been discharging oocysts and/or infected with *Caryospora* or *Eumonospora* coccidian species. Items listed include current binomial, authority, common name, and host taxonomic family.

***Accipiter striatus* Vieillot, 1808, sharp-shinned hawk (Accipitridae)**
Eumonospora petersoni (McAllister et al., 2013b) Chou et al., 2020

***Agkistrodon contortrix* L., 1766, copperhead (Viperidae)**
Caryospora bigenetica Wacha & Christiansen, 1982

***Ahaetulla nasuta* (Lacépède, 1789), long-nosed vine snake (Colubridae)**
Caryospora ahaetullae Modrý & Koudela, 1994
Caryospora veselyi Modrý & Koudela, 1998

***Ahaetulla prasina* (Boie, 1827), Gunther's or oriental whipsnake (Colubridae)**
Caryospora ahaetullae Modrý & Koudela, 1994

***Anolis carolinensis* Voigt, 1832, North American green anole (Anolidae)**
Caryospora ernsti Upton et al., 1984b
Caryospora natchitochesensis McAllister et al., 2014

***Aquila chrysaetos* (L., 1758), golden eagle (Accipitridae)**
Eumonospora aquilae (Volf et al., 2000) Chou et al., 2020
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020
Eumonospora sp. 2 of Volf & Modrý, 1998 n. comb.

***Athene noctua* (Scopoli, 1769), little owl (Strigidae)**
Caryospora sp. of Wetzel & Enigk, 1939 (syn. non *Caryospora falconis* Wetzel and Enigk, 1939)
Eumonospora falconis (Wetzel & Enigk, 1937) Chou et al., 2020
Eumonospora henryae (emend. Pellérdy, 1974) Chou et al., 2020 (syns. *Isospora henryi* Yakimoff & Matikaschwili, 1932; *Eumonospora tremula* Allen, 1933; *Caryospora henryi* (Yakimoff & Matikaschwili, 1932) Yakimoff & Matschulsky, 1936; *Caryospora henryae* (Yakimoff & Matschulsky, 1936); Pellérdy, 1974)
Eumonospora mochogalegoi (Cardozo et al., 2017) Chou et al., 2020 (syn. *Avispora mochogalegoi* Cardozo et al., 2017)

***Atheris ceratophora* Werner, 1896 (syn. *Atheris ceratophorus* Werner, 1895 of Modrý et al., 2002), horned bush viper (Viperidae)**
Caryospora matatu Modrý et al., 2002

***Atheris nitschei* Tornier, 1902, Niche's bush viper (Viperidae)**
Caryospora sp. 1 of Modrý, 1998
Caryospora sp. 2 of Koudela et al., 2000

***Boaedon fuliginosus* (Boie, 1827), African or brown house snake (Lamprophiidae)**
Caryospora hermae Bray, 1960

***Boiga dendrophila* (Boie, 1827), mangrove or gold-ringed cat snake (Colubridae)**
Caryospora kalimantanensis Modrý & Koudela, 1997

***Bothriechis aurifer* Salvin, 1860, yellow-blotched palm pit viper (Viperidae)**
Caryospora bothriechis Seville et al., 2005

***Bothriechis lateralis* Peters, 1862, coffee palm viper (Viperidae)**
Caryospora jararacae (Carini, 1939) Lainson et al., 1991 (syn. *Caryospora jaracae* Carini, 1939 *lapsus calami*)
Caryospora sp. of Upton & Sundermann, 1990

***Bothrops atrox* (L., 1758), fer-de-lance (Viperidae)**
Caryospora jararacae (Carini, 1939) Lainson et al., 1991 (syn. *Caryospora jaracae* Carini, 1939 *lapsus calami*)

***Bothrops jararaca* (Wied-Neuwied, 1824), jararaca (Viperidae)**
Caryospora jararacae (Carini, 1939) Lainson et al., 1991 (syn. *Caryospora jaracae* Carini, 1939 *lapsus calami*)
Caryospora sp. of Fernandes-Grego et al., 2004
Caryospora sp. of Hoge-1 (*Bothrops* spp.), 1991

***Bothrops neuwiedi* Wagler, 1824, Wied's lance-head (Viperidae)**
Caryospora sp. of Hoge-1 (*Bothrops* spp.), 1991

***Bubo bubo* (L., 1758), Eurasian eagle-owl (Strigidae)**
Eumospora bubonis (Cawthorn & Stockdale, 1981) Chou et al., 2020
Eumonospora henryae (emend. Pellérdy, 1974) Chou et al., 2020 (syn. *Isospora henryi* Yakimoff & Matikaschwili, 1932; *Eumonospora tremula* Allen, 1933; *Caryospora henryi* (Yakimoff & Matikaschwili, 1932) Yakimoff & Matschulsky, 1936; *Caryospora henryae* (Yakimoff & Matschulsky, 1936); Pellérdy, 1974)

***Bubo scandiacus* (L., 1758) (syn. *Nyctea scandiaca* (L., 1758)) snowy owl (Strigidae)**
Eumonospora henryae (emend. Pellérdy, 1974) Chou et al., 2020 (syn. *Isospora henryi* Yakimoff & Matikaschwili, 1932; *Eumonospora tremula* Allen, 1933; *Caryospora henryi* (Yakimoff & Matikaschwili, 1932) Yakimoff & Matschulsky, 1936; *Caryospora henryae* (Yakimoff & Matschulskyi, 1936) Pellérdy, 1974)

Table 2. Alphabetical list of all vertebrate host species documented to have been discharging oocysts and/or infected with *Caryospora* or *Eumonospora* coccidian species. Items listed include current binomial, authority, common name, and host taxonomic family (*continued*).

Eumonospora kutzeri (Böer, 1982) Chou et al., 2020 (syn. *Caryospora henryi* of Yakimoff & Matschulsky, 1936, in part; *Caryospora* sp. of Kutzer et al., 1980; *Caryospora falconis* of Scheller & Rodler, 1971
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020

***Bubo virginianus* (Gmelin, 1788), great horned owl (Strigidae)**
Eumonospora bubonis (Cawthorn & Stockdale, 1981) Chou et al., 2020

***Buteo jamaicensis* (Gemlin, 1788), red-tailed hawk (Accipitridae)**
Eumonospora lindsayi (Upton, Campbell, et al., 1990) Chou et al., 2020

***Buteo jamaicensis borealis* (Gemlin, 1788), eastern red-tailed hawk (Accipitridae)**
Eumonospora uptoni (Lindsay & Blagburn, 1986) Chou et al., 2020

***Buteo magnirostris* (Gmelin, J.F., 1788), roadside hawk (Accipitridae)**
Eumonospora arcayae (Volcán & Medrano, 1984) Chou et al., 2020 (syn. *Caryospora* sp. of Upton & Sundermann, 1990)

***Buteo platypterus* (Vieillot, 1823), broad-winged hawk (Accipitridae)**
Eumonospora arcayae (Volcán & Medrano, 1984) Chou et al., 2020 (syn. *Caryospora* sp. of Upton & Sundermann, 1990)

***Buteo swainsoni* Bonaparte, 1838, Swainson's hawk (Accipitridae)**
Eumonospora kansasensis (Upton, Campbell, et al., 1990) Chou et al., 2020 (syn. *Caryospora* sp. of Upton & Sundermann, 1990)

***Calloselasma rhodostoma* (Kuhl, 1824), Malayan pit viper (Viperidae)**
Caryospora sp. 1 of Koudela et al., 2000
Caryospora sp. 2 of Modrý, 1998

***Canis familiaris* L. 1758, Domestic dog (Canidae)**
Caryospora spp. (in dogs) of Marcone, 1908 and others

***Casarea dussumieri* (Schlegel, 1837), Round Island boa (Bolyeridae)**
Caryospora durrelli Daszak et al., 2011a, b
Caryospora sp. of Daszak, 1995

***Cathares aura* (L., 1758), Turkey vulture (Catharidae)**
Caryospora tremula (Allen, 1933) Hoare, 1934
Eumonospora henryae (emend. Pellérdy, 1974) Chou et al., 2020 (syns. *Isospora henryi* Yakimoff & Matikaschwili, 1932; *Eumonospora tremula* Allen, 1933; *Caryospora henryi* (Yakimoff & Matikaschwili, 1932) Yakimoff & Matschulsky, 1936; *Caryospora henryae* (Yakimoff & Matschulsky, 1936); Pellérdy, 1974)
Eumonospora tremula (Allen, 1933) Chou et al., 2020 (syn. *Eumonospora tremula* Allen, 1933)

***Causus maculatus* (Hallowell, 1842), spotted night adder (Viperidae)**
Caryospora maculatus Upton, Freed & Freed, 1992

***Chelonia mydas mydas* (L., 1758), green turtle (Cheloniidae)**
Caryospora cheloniae Leibovitz et al., 1978 (syn. *Caryospora* sp. of Robell, 1974)

***Chlamydotis macqueenii* (Gray, J.E., 1832), MacQueen's bustard (Otididae)**
Eumonospora megafalconis (Klüh, 1994) Chou et al., 2020

***Chlamydotis undulata* (Jacquin, 1784), Houbara bustard (Otididae)**
Eumonospora megafalconis (Klüh, 1994) Chou et al., 2020

***Circus aeruginosus* (L., 1758), western marsh harrier (Accipitridae)**
Eumonospora circi (Volf et al., 2000) Chou et al., 2020
Eumonospora sp. 1 of Volf & Modrý, 1998 n. comb.

***Coluber constrictor priapus* Dunn & Wood, 1939, southern black racer (Colubridae)**
Caryospora masticophis Upton et al., 1994

***Coniophanes imperialis* (Kennicott in Baird, 1859), black-striped snake (Colubridae)**
Caryospora coniophanis Seville et al., 2005

***Conophis imperialis* (Duméril, Bibron and Duméril, 1854), road guarder snake (Colubridae)**
Caryospora conophae Seville et al., 2005

***Conophis lineatus* (Duméril, Bibron & Duméril, 1854), road guarder snake (Colubridae)**
Caryospora mayorum Seville et al., 2005

***Corallus cainus* (L., 1758), emerald tree boa (Boidae)**
Caryospora corallae Matuschka, 1984b

***Crotalus adamanteus* Palisot de Beauvois, 1799, eastern diamondback rattlesnake (Viperidae)**
Caryospora bigenetica Wacha & Christiansen, 1982

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***Crotalus atrox* Baird and Giraud, 1853, western diamondback rattlesnake (Viperidae)**
Caryospora bigenetica Wacha & Christiansen, 1982

***Crotalus durissus* L., 1758, cascabel rattlesnake (Viperidae)**
Caryospora sp. of Hoge-2 (*Crotalus* sp.), 1991

***Crotalus horridus* L. 1758, timber or cane-brake rattlesnake (Viperidae)**
Caryospora bigenetica Wacha & Christiansen, 1982

***Daboia palestinae* (Werner, 1938) (syn. *Vipera palestinae* Werner, 1938), Palestine viper (Viperidae)**
Caryospora simplex Léger, 1911 (syn. *Karyospora simplex* Léger, 1904 (*lapsus*))

***Daboia russelii* (Shaw & Nodder, 1797) (syn. *Vipera russelii* Strauch, 1869), Russell's viper (Viperidae)**
Caryospora simplex Léger, 1911 (syn. *Karyospora simplex* Léger, 1904 (*lapsus*))

***Dacelo novaeguineae* (Hermann, 1783), laughing kookaburra (Alcedinidae)**
Eumonospora daceloe (Yang et al., 2014) Chou et al., 2020

***Demansia psammophis* (Schlegel, 1857), yellow-faced whip snake (Elapidae)**
Caryospora demansiae Cannon, 1967

***Dendrelaphis punctulatus* (Gray 1826), common tree snake (Colubridae)**
Caryospora dendrelaphis Cannon & Rzepczyk, 1974

***Dendroaspis angusticeps* (Smith, 1849), green mamba (Elapidae)**
Caryospora regentensis Daszak & Ball, 2001a, b

***Dendroaspis viridis* (Hallowell, 1844), western green mamba (Elapidae)**
Caryospora regentensis Daszak & Ball, 2001a, b

***Diphyllodes magnificus* (Pennant, 1781), magnificent bird-of-paradise (Paradisaeidae)**
Caryospora sp. of Varghese & Yayabu, 1981

***Dolichophis jugularis* (L., 1758) (syn. *Coluber jugularis* L., 1758), large whip snake (Colubridae)**
Caryospora colubris Matuschka, 1984b

***Echis carinatus* (Schneider, 1801), saw-scaled or African carpet viper (Viperidae)**
Caryospora saudiarabiensis (Modrý et al., 1999) Duszynski & Upton, 2010 (syn. *Caryospora "maxima"* Modrý et al., 1999 of Alyousif et al., 2004)

***Echis coloratus* Günther, 1878, Palestime saw-scaled viper (Viperidae)**
Caryospora maxima Modrý et al., 1999

***Eirenis decemlineatus* (Duméril, Bibron et Duméril, 1854), [no English common name] (Colubridae)**
Caryospora colubris Matuschka, 1984b

***Enhydris enhydris* Schneider, 1799, rainbow or striped water snake (Colubridae)**
Caryospora bengalensis Mandel, 1976

***Epicrates cencheria* (L., 1758), rainbow boa (Boidae)**
Caryospora epicrati Lainson et al., 1991, emend. Modrý, 1998 (syn. *Caryospora epicratesi* Lainson et al., 1991)

***Erithacus rubecula* (L., 1758), European robin (Muscicapidae)**
Caryospora jiroveci Černá, 1976

***Erythrolamprus poecilogyrus* (Weid-Neuwied, 1824), cobra verde (Colubridae)**
Caryospora brasiliensis Carini, 1932

***Falco biarmicus* Temminck, 1825, lanner falcon (Falconidae)**
Eumonospora biarmicusis (Alyousif et al., 2011) Chou et al., 2020
Eumonospora kutzeri (Böer, 1982) Chou et al., 2020 (syns. *Caryospora henryi* of Yakimoff & Matschulsky, 1936, in part; *Caryospora* sp. of Kutzer et al., 1980; *Caryospora falconis* of Scheller & Rodler, 1971)
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020

***Falco cherrug* Gray, J.E., 1834, saker falcon (Falconidae)**
Eumonospora cherrughi (Alfaleh et al., 2013) Chou et al., 2020
Eumonospora kutzeri (Böer, 1982) Chou et al., 2020 (syns. *Caryospora henryi* of Yakimoff & Matschulsky, 1936, in part; *Caryospora* sp. of Kutzer et al., 1980; *Caryospora falconis* of Scheller & Rodler, 1971)
Eumonospora megafalconis (Klüh, 1994) Chou et al., 2020
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020

***Falco columbarius* L., 1758, merlin (Falconidae)**
Eumonospora henryae (emend. Pellérdy, 1974) Chou et al., 2020 (syns. *Isospora henryi* Yakimoff & Matikaschwili, 1932; *Eumonospora tremula* Allen, 1933; *Caryospora henryi* (Yakimoff & Matikaschwili, 1932) Yakimoff & Matschulsky, 1936; *Caryospora henryae* (Yakimoff & Matschulsky, 1936); Pellérdy, 1974)

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Eumonospora neofalconis (Böer, 1982) Chou et al., 2020

***Falco jugger* Gray, J.E., 1834, laggar falcon (Falconidae)**
Eumonospora kutzeri (Böer, 1982) Chou et al., 2020 (syns. *Caryospora henryi* of Yakimoff & Matschulsky, 1936, in part; *Caryospora* sp. of Kutzer et al., 1980; *Caryospora falconis* of Scheller & Rodler, 1971)

***Falco mexicanus* Schlegel, 1850, prairie falcon (Falconidae)**
Eumonospora kutzeri (Böer, 1982) Chou et al., 2020 (syns. *Caryospora henryi* of Yakimoff & Matschulsky, 1936, in part; *Caryospora* sp. of Kutzer et al., 1980; *Caryospora falconis* of Scheller & Rodler, 1971)
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020

***Falco peregrinus* Tunstall, 1771, peregrine falcon (Falconidae)**
Eumonospora falconis (Wetzel & Enigk, 1937) Chou et al., 2020
Eumonospora kutzeri (Böer, 1982) Chou et al., 2020 (syns. *Caryospora henryi* of Yakimoff & Matschulsky, 1936, in part; *Caryospora* sp. of Kutzer et al., 1980; *Caryospora falconis* of Scheller & Rodler, 1971)
Eumonospora megafalconis (Klüh, 1994) Chou et al., 2020
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020

***Falco peregrinus peregrinator* (hybrid), black shaheen (Falconidae)**
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020

***Falco rusticolus* L., 1758, gyrfalcon (Falconidae)**
Eumonospora kutzeri (Böer, 1982) Chou et al., 2020 (syns. *Caryospora henryi* of Yakimoff & Matschulsky, 1936, in part; *Caryospora* sp. of Kutzer et al., 1980; *Caryospora falconis* of Scheller & Rodler, 1971)
Eumonospora megafalconis (Klüh, 1994) Chou et al., 2020
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020

***Falco subbuteo* L., 1758, Eurasian hobby (Falconidae)**
Eumonospora falconis (Wetzel & Enigk, 1937) Chou et al., 2020
Eumonospora henryae (emend. Pellérdy, 1974) Chou et al., 2020 (syns. *Isospora henryi* Yakimoff & Matikaschwili, 1932; *Eumonospora tremula* Allen, 1933; *Caryospora henryi* (Yakimoff & Matikaschwili, 1932) Yakimoff & Matschulsky, 1936; *Caryospora henryae* (Yakimoff & Matschulsky, 1936); Pellérdy, 1974)
Eumonospora kutzeri (Böer, 1982) Chou et al., 2020 (syns. *Caryospora henryi* of Yakimoff & Matschulsky, 1936, in part; *Caryospora* sp. of Kutzer et al., 1980; *Caryospora falconis* of Scheller & Rodler, 1971)
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020

***Falco tinnunculus* L., 1758, European kestrel (Falconidae)**
Eumonospora boeri (Klüh, 1994) Chou et al., 2020 (syn. *Caryospora* sp. Kutzer et al., 1980)
Eumonospora falconis (Wetzel & Enigk, 1937) Chou et al., 2020
Eumonospora henryae (emend. Pellérdy, 1974) Chou et al., 2020 (syns. *Isospora henryi* Yakimoff & Matikaschwili, 1932; *Eumonospora tremula* Allen, 1933; *Caryospora henryi* (Yakimoff & Matikaschwili, 1932) Yakimoff & Matschulsky, 1936; *Caryospora henryae* (Yakimoff & Matschulsky, 1936); Pellérdy, 1974).
Eumonospora kutzeri (Böer, 1982) Chou et al., 2020 (syns. *Caryospora henryi* of Yakimoff & Matschulsky, 1936, in part; *Caryospora* sp. of Kutzer et al., 1980; *Caryospora falconis* of Scheller & Rodler, 1971)
Eumonospora megafalconis (Klüh, 1994) Chou et al., 2020 (experimentally)
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020
Eumonospora peneireiroi (Cardozo et al., 2016) Chou et al., 2020
Eumonospora sp. of Cringoli, Quesada & Papparella, 1991 n. comb.

***Gecko gecko* (L., 1758), Tokay gecko (Gekkonidae)**
Caryospora gekkonis Chakravarty & Kar 1947

Ger-saker hybrid (Falconidae)
Eumonospora megafalconis (Klüh, 1994) Chou et al., 2020

***Grallina cyanoleuca* (Latham, 1801), Magpie lark (Monarchidae)**
Caryospora sp. of Liu et al., 2019

***Haliaeetus leucocephalus* (L.,1766), bald eagle (Accipitridae)**
Eumonospora hanebrinki (McAllister et al., 2013a) Chou et al., 2020

***Hemorrhois hippocrepis* (L., 1758) (syn. *Coluber hippocrepis* L., 1758), horseshoe whip snake (Colubridae)**
Caryospora colubris Matuschka, 1984b

Table 2. Alphabetical list of all vertebrate host species documented to have been discharging oocysts and/or infected with *Caryospora* or *Eumonospora* coccidian species. Items listed include current binomial, authority, common name, and host taxonomic family (*continued*).

***Hemorrhois ravergieri* Ménétries, 1832 (syn. *Coluber ravergieri nummifer* Reuss, 1843), spotted whip snake (Colubridae)**
Caryospora zuckermanae of Bray 1960

***Heterodon platirhinos* Letreille, 1801, eastern hognose snake (Colubridae)**
Caryospora lampropeltis Anderson et al., 1968

***Hierophis* (syn. *Coluber*) *viridiflavus* (Lacépède, 1798), green or western whip snake (Colubridae)**
Caryospora colubris Matuschka, 1984b

***Lampropeltis calligaster* (Harlan, 1827), prairie kingsnake (Colubridae)**
Caryospora duszynskii Upton et al., 1984a
Caryospora lampropeltis Anderson et al., 1968

***Lampropeltis holbrooki* Stejneger, 1902, speckled kingsnake (Colubridae)**
Caryospora duszynskii Upton et al., 1984a
Caryospora lampropeltis Anderson et al., 1968

***Lampropeltis triangulum* (Lacépède, 1789), eastern milksnake (Colubridae)**
Caryospora duszynskii Upton et al., 1984a
Caryospora guatemalensis Seville et al., 2005
Caryospora lampropeltis Anderson et al., 1968

***Larus argentatus* Pontoppidan, 1763, European herring gull (Laridae)**
Eumonospora argentati (Schwalbach, 1959) Chou et al., 2020
Eumonospora undata (Schwalbach, 1959) Chou et al., 2020 (syn. *Caryospora undulata* Poelma & Strik, 1966 (*lapsus*)).

***Leimadophis poecilogyrus schotti* (Schlegel, 1837), cobra-corredeira (Colubridae)**
Caryospora brasiliensis Carini, 1932

***Leioheterodon madagascariensis* Duméril & Bibron, 1854, Madagascar hog-nose snake (Colubridae)**
Caryospora minuta Upton, Freed, et al., 1990
Caryospora serpentis Upton, Freed, et al., 1990

***Liopholidophis stumpffi* (Boettger, 1881), Malagasy colubrid (Colubridae)**
Caryospora barnardae Upton, Freed, et al., 1990

***Madagascarophis colubrinus* (Schlegel, 1837), Madagascar cat-eye snake (Pseudoxyrhophiidae)**
Caryospora brygooi Upton, Freed, et al., 1990
Caryospora madagascariensis Upton, Freed, et al., 1990
Caryospora serpentis Upton, Freed, et al., 1990

***Masticophis flagellum* (Shaw, 1802), coachwhip (Colubridae)**
Caryospora duszynskii Upton et al., 1984a

***Masticophis flagellum flagellum* (Shaw, 1837), eastern coachwhip (Colubridae)**
Caryospora masticophis Upton et al., 1994

***Masticophis mentovarius* (Duméril et al., 1854), Neotropical whip snake (Colubridae)**
Caryospora zacapensis Seville et al., 2005

***Microtus pennsylvanicus* (Ord, 1815), meadow vole (Cricetidae)**
Eumonospora microti (Saxe et al., 1960) Chou et al., 2020 (syns. *Caryospora* sp. Saxe, 1952; *Caryospora microti* Saxe et al., 1960)

***Micrurus spixii spixii* Schmidt & Walker, 1943, Amazonian coral snake (Elapidae)**
Caryospora constanciae Lainson et al., 1991
Caryospora micruri Lainson et al., 1991

***Milvus migrans* (Boddaert, 1783), black kite (Accipitridae)**
Caryospora sp. of Yakimoff & Matschoulsky, 1936 (syn. *Caryospora henryae*, ovoidal form, in part, of Yakimoff & Matschoulsky, 1936)
Caryospora sp. of Yakimoff & Matschoulsky, 1936 (syn. *Caryospora henryae*, round form, in part, of Yakimoff & Matschoulsky, 1936)
Eumonospora henryae (emend. Pellérdy, 1974) Chou et al., 2020 (syns. *Isospora henryi* Yakimoff & Matikaschwili, 1932; *Eumonospora tremula* Allen, 1933; *Caryospora henryi* (Yakimoff & Matikaschwili, 1932) Yakimoff & Matschulsky 1936; *Caryospora henryae* (Yakimoff & Matschulsky, 1936); Pellérdy, 1974)

***Mimophis mahfalensis* (Grandidier, 1867), Malagasy colubrid (Colubridae)**
Caryospora madagascariensis Upton, Freed, et al., 1990
Caryospora serpentis Upton, Freed, et al., 1990

***Montivipera xanthina* (Gray, 1849) (syn. *Vipera xanthina* Gray, 1849), Ottoman or coastal viper (Viperidae)**
Caryospora simplex Léger, 1911 (syn. *Karyospora simplex* Léger, 1904 (*lapsus*))

***Naja naja* (L., 1758), common or spectacled cobra (Elapidae)**
Caryospora cobrae Nandi, 1985

Table 2. Alphabetical list of all vertebrate host species documented to have been discharging oocysts and/or infected with *Caryospora* or *Eumonospora* coccidian species. Items listed include current binomial, authority, common name, and host taxonomic family (*continued*).

***Naja nigricollis* Reinhardt, 1843, black-necked spitting cobra (Elapidae)**
Caryospora najae Matuschka, 1982

***Oxyrhopus petola digitalis* (Reuss, 1834), forest flame snake (Colubridae)**
Caryospora carajasensis Lainson et al., 1991
Caryospora paraensis Lainson et al., 1991

***Pantherophis emoryi* (Baird et Girard, 1853), Great Plains rat snake (Colubridae)**
Caryospora duszynskii Upton et al., 1984a

***Pantherophis guttatus* (L., 1766) (syn. *Coluber guttata* L., 1766), eastern corn snake (Colubridae)**
Caryospora duszynskii Upton et al., 1984a

***Pantherophis obsoletus* (Say, 1823) (syn. *Coluber obsoletus* Say, 1823), black rat snake (Colubridae)**
Caryospora duszynskii Upton et al., 1984a

***Philodryas aestivus* (Duméril, Bibron and Duméril, 1854), Brazilian or common green racer (syn. *Dryophylax aestivus* Duméril, Bibron and Duméril, 1854) (Colubridae)**
Caryospora brasiliensis Carini, 1932

***Philodryas nattereri* (Steindachner, 1870), Paraguay green racer (Colubridae)**
Caryospora brasiliensis Carini, 1932

***Philodryas olfersii* (Lichtenstein, 1823), Lichtenstein's green racer (Colubridae)**
Caryospora brasiliensis Carini, 1932
Caryospora olfersii Viana et al., 2013

***Philothamnus heterodermus* Hallowell, 1857, emerald or variable green snake (Colubridae)**
Caryospora heterodermus Upton, Freed & Freed, 1992

***Platyceps najadum* (Eichwald, 1831) (syn. *Coluber najadum* Schmidt, 1939), Dahl's whip snake (Colubridae)**
Caryospora najadae Matuschka, 1986a

***Podargus strigoides* (Latham, 1801), Tawny frogmouth (Podargidae)**
Eumonospora sp. of Montali et al., 2005

***Psammophis orientalis* Broadley, 1977, eastern stripe-bellied sand snake (Colubridae)**
Caryospora sp. I of Šlapeta et al., 2003
Caryospora sp. II of Šlapeta et al., 2003

***Psammophis phillipsii* Hallowell, 1844 (syn. *P. sibilans phillipsi* Loveridge, 1840), hissing, olive or western sand snake (Psammophiidae)**
Caryospora hermae Bray, 1960
Caryospora psammophi Bray, 1960
Caryospora weyerae Bray, 1960

***Psammophis schokari* (Forskål, 1775), Forskål's sand snake (Psammophiidae)**
Caryospora maxima Modrý et al., 1999

***Psammophis sibilans* (L., 1758), Egyptian hissing sand snake (Psammophiidae)**
Caryospora hermae Bray, 1960
Caryospora legeri Hoare, 1933 (syn. *Caryospora legeri* Matubayashi, 1937 (*lapsus*))

***Ptilosis leucotis* (Temminck, 1820), northern white-faced owl (Strigidae)**
Eumonospora henryae (emend. Pellérdy, 1974) Chou et al., 2020 (syn. *Isospora henryi* Yakimoff & Matikaschwili, 1932; *Eumonospora tremula* Allen, 1933; *Caryospora henryi* (Yakimoff & Matikaschwili, 1932) Yakimoff & Matschulsky, 1936; *Caryospora henryae* (Yakimoff & Matschulsky, 1936); Pellérdy, 1974)

***Ptiloxena atroviolacea* (d'Orbigny, 1839) (syn. *Dives atroviolaceus*), Cuban blackbird or toti (Icteridae)**
Eumonospora gloriae (Pellérdy, 1967) n. comb.

***Python* sp. (Pythonidae)**
Caryospora sp. of Frye, 1981

***Rhabdophis tigrinus* (Boie, 1826) (syns. *Natrix tigrina* [Boie, 1826]; *Natrix tigrine* Stejneger, 1907), Yamakagashi snake of Japan or tiger keelback (Colubridae)**
Caryospora japonicum Matubayashi, 1936

***Rupornis magnirostris* (Gmelin, J.F., 1788) (syn. *Falco magnirostris* Gmelin, J.F., 1788) (Accipitridae)**
Eumonospora arcayae (Volcán & Medrano, 1984) Chou et al., 2020 (syn. *Caryospora* sp. of Upton & Sundermann, 1990)

***Siphlophis pulcher* (Raddi, 1820), Guanabara spotted night snake (Dipsadidae)**
Caryospora ceadsensis Tobias de Santana Miglionico & Viana, 2017

***Sistrurus catenaus* (Rafinesque, 1818), massasauga (natural and experimental) (Viperidae)**
Caryospora bigenetica Wacha & Christiansen, 1982

Table 2. Alphabetical list of all vertebrate host species documented to have been discharging oocysts and/or infected with *Caryospora* or *Eumonospora* coccidian species. Items listed include current binomial, authority, common name, and host taxonomic family (*continued*).

***Sistrurus miliaris* L., 1766, Pigmy rattlesnake (Viperidae)**
Caryospora bigenetica Wacha & Christiansen, 1982

***Spilotes sulphureus sulphureus* (Wagler, 1824) (syn. *Pseustes sulphureus sulphureus* Beebe, 1946), yellow-bellied hissing or Amazon puffing snake (Colubridae)**
Caryospora pseustesi Lainson et al., 1991

***Strix nebulosi* Foster, 1772, great gray owl (Strigidae)**
Eumonospora henryae (emend. Pellérdy, 1974) Chou et al., 2020 (syns. *Isospora henryi* Yakimoff & Matikaschwili, 1932; *Eumonospora tremula* Allen, 1933; *Caryospora henryi* (Yakimoff & Matikaschwili, 1932) Yakimoff & Matschulsky, 1936; *Caryospora henryae* (Yakimoff & Matschulsky, 1936); Pellérdy, 1974)

***Tantilla gracilis* Baird and Girard, 1853, flat-head snake (Colubridae)**
Caryospora choctawensis McAllister et al., 2013
Caryospora gracilis Upton et al., 1992
Caryospora sargentae McAllister et al., 2022

***Tantilla relicta* Telford, 1966, Florida crowned snake (Colubridae)**
Caryospora relictae Telford, 1997
Caryospora tantillae Telford, 1997

***Telescopus fallax* (Fleischmann, 1831), European or Mediterranean cat snake (Colubridae)**
Caryospora telescopis Matuschka, 1986

***Tomodon dorsatus* Duméril, Bibron et Duméril, 1854, pampas snake (Colubridae)**
Caryospora sp. of Hoge-3 (*Tomodon* sp.), 1991

***Tyto alba* (Scopoli, 1769), barn owl (Tytonidae)**
Eumonospora strigis (Gottschalk, 1972) Chou et al., 2020

***Uria aalge aalge* (Pontoppian, 1763), common murre or guillemot (Alcidae)**
Eumonospora undata (Schwalbach, 1959) Chou et al., 2020 (syn. *Caryospora undulata* Poelma & Strik, 1966 (*lapsus*))

***Varanus niloticus* (L., 1758), Nile monitor (Varanidae)**
Caryospora sp. 4 of Koudela et al., 2000

***Varanus* (*Polydaedalus*) *ornatus* (Daudin, 1803), ornate monitor (Varanidae)**
Caryospora varaniornati Modrý et al., 2001

***Varanus* sp. Merrem, 1820, carnivorous lizard (Varanidae)**
Caryospora varani of Kaur & Oberoi, 1987

***Vipera ammodytes* (L., 1758), nose-horned or sand viper (Viperidae)**
Caryospora simplex Léger, 1911 (syn. *Karyospora simplex* Léger, 1904 (*lapsus*))

***Vipera aspis* (L., 1758), European asp or asp viper (Viperidae)**
Caryospora simplex Léger, 1911 (syn. *Karyospora simplex* Léger, 1904 (*lapsus*))

***Vipera berus* (L., 1758), adder or northern viper (Viperidae)**
Caryospora simplex Léger, 1911 (syn. *Karyospora simplex* Léger, 1904 (*lapsus*))

***Vipera kaznakovi* Nikolsky, 1909, Caucasus viper (Viperidae)**
Caryospora simplex Léger, 1911 (syn. *Karyospora simplex* Léger, 1904 (*lapsus*))
Caryospora sp. of Matuschka, 1986b

***Vipera ursinii* (Bonaparte, 1835), Ursini's viper (Viperidae)**
Caryospora sp. 3 of Koudela et al., 2000

***Xenoxybelis argenteus* (Daudin, 1803), striped sharp-nosed snake (syn. *Coluber argenteus* Daudin, 1803) (Colubridae)**
Caryospora peruensis Upton et al., 1989

Table 3. Alphabetical list of countries from which *Caryospora* and *Eumonospora* species have been described through 2023

Africa (countries)
- Benin (1 of 16 West African countries)
  - *Caryospora* sp. 4 of Koudela et al., 2000
  - *Caryospora varaniornati* Modrý et al., 2001
- Cameroon
  - *Caryospora heterodermus* Upton, Freed & Freed, 1992
  - *Caryospora maculatus* Upton, Freed & Freed, 1992
- "East Africa"
  - *Caryospora najae* Matuschka, 1982
- Kenya
  - *Caryospora regentensis* Daszak & Ball, 2001a, b
  - *Caryospora* sp. I of Šlapeta et al., 2003
  - *Caryospora* sp. II of Šlapeta et al., 2003
- Liberia
  - *Caryospora hermae* Bray, 1960
  - *Caryospora psammophi* Bray, 1960
  - *Caryospora weyerae* Bray, 1960
- Tanzania
  - *Caryospora matatu* Modrý et al., 2002
- Uganda
  - *Caryospora legeri* Hoare, 1933
  - *Caryospora* sp. 2 of Koudela et al., 2000
  - *Caryospora* sp. 1 of Modrý, 1998
- Zambia
  - *Caryospora hermae* Bray, 1960
  - *Caryospora psammophi* Bray, 1960
  - *Caryospora weyerae* Bray, 1960

Australia (states)
- Queensland
  - *Caryospora demansiae* Cannon, 1967
  - *Caryospora dendrelaphis* Cannon and Rzepczyk, 1974
  - *Eumonospora* sp. of Montali et al., 2005 n. comb.
- Western Australia
  - *Caryospora* sp. of Liu et al., 2020
  - *Eumonospora daceloe* (Yang et al., 2014) Chou et al., 2020

Austria
- *Eumonospora argentati* (Schwalbach, 1959) Chou et al., 2020

Brazil (states)
- Amazonas
  - *Caryospora jararacae* (Carini, 1939) Lainson et al., 1991
- Pará
  - *Caryospora carajasensis* Lainson et al., 1991
  - *Caryospora paraensis* Lainson et al., 1991
  - *Caryospora pseustesi* Lainson et al., 1991
- Rio de Janeiro
  - *Caryospora ceadsensis* Tobias de Santana Miglionico & Viana, 2017
  - *Caryospora olfersii* Viana et al., 2013
- Rondônia
  - *Caryospora constanciae* Lainson et al., 1991
  - *Caryospora epicrati* Lainson et al., 1991, emended Modrý, 1998
  - *Caryospora micruri* Lainson et al., 1991
- São Paulo
  - *Caryospora brasiliensis* Carini, 1932
  - *Caryospora jararacae* (Carini, 1939) Lainson et al., 1991
  - *Caryospora* sp. of Fernandes-Grego et al., 2004
  - *Caryospora* sp. of Hoge-1 (*Bothrops* spp.), 1991
  - *Caryospora* sp. of Hoge-2 (*Crotalus* sp.), 1991
  - *Caryospora* sp. of Hoge-3 (*Tomodon* sp.), 1991

British West Indies (Grand Cayman)
- *Caryospora cheloniae* Leibovitz et al., 1978

Bulgaria
- *Caryospora simplex* Léger, 1911

Canada (provinces)
- Saskatchewan
  - *Eumonospora bubonis* (Cawthorn & Stockdale, 1981) Chou et al., 2020

Cuba
- *Eumonospora gloriae* (Pellérdy, 1967) n. comb.

Czech Republic
- *Caryospora bigenetica* Wacha & Christiansen, 1982
- *Caryospora duszynskii* Upton et al., 1984a
- *Caryospora jiroveci* Černá, 1976
- *Caryospora kalimantanensis* Modrý & Koudela, 1997
- *Caryospora simplex* Léger, 1911
- *Caryospora varaniornati* Modrý et al., 2001
- *Eumonospora aquilae* (Volf et al., 2000) Chou et al., 2020
- *Eumonospora circi* (Volf et al., 2000) Chou et al., 2020
- *Eumonospora kutzeri* (Böer, 1982) Chou et al., 2020
- *Eumonospora neofalconis* (Böer, 1982) Chou et al., 2020
- *Eumonospora* sp. 1 of Volf & Modrý, 1998 n. comb.
- *Eumonospora* sp. 2 of Volf & Modrý, 1998 n. comb.

France
- French Guayana (territory)
  - *Caryospora corallae* Matuschka, 1984b
- Dauphine (former Province in SE France)
  - *Caryospora simplex* Léger, 1911

Germany
- *Caryospora* sp. of Wetzel and Enigk, 1939
- *Eumonospora argentati* (Schwalbach, 1959) Chou et al., 2020
- *Eumonospora boeri* (Klüh, 1994) Chou et al., 2020
- *Eumonospora falconis* (Wetzel & Enigk, 1937) Chou et al., 2020

Table 3. Alphabetical list of countries from which *Caryospora* and *Eumonospora* species have been described through 2023 (*continued*)

Eumonospora kutzeri (Böer, 1982) Chou et al., 2020
Eumonospora megafalconis (Klüh, 1994) Chou et al., 2020
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020
Eumonospora strigis (Gottschalk, 1972) Chou et al., 2020
Eumonospora undata (Schwalbach, 1959) Chou et al., 2020

Greece
Caryospora telescopis Matuschka, 1986b

Guatemala
Caryospora bothriechis Seville et al., 2005
Caryospora coniophanis Seville et al., 2005
Caryospora conophae Seville et al., 2005
Caryospora guatemalensis Seville et al., 2005
Caryospora mayorum Seville et al., 2005
Caryospora zacapensis Seville et al., 2005

India
Caryospora ahaetullae Modrý & Koudela, 1994
Caryospora bengalensis Mandal, 1976
Caryospora cobrae Nandi, 1985
Caryospora gekkonis Chakravarty & Kar, 1947
Caryospora varani of Kaur & Oberoi, 1987
Caryospora veselyi Modrý & Koudela, 1998

Indonesia
Kalimantan (Borneo)
Caryospora kalimantanensis Modrý & Koudela, 1997

Israel
Caryospora colubris Matuschka, 1984b
Caryospora najadae Matuschka, 1986a
Caryospora zuckermanae of Bray, 1960

Italy
Caryospora colubris Matuschka, 1984b
Caryospora spp. in dogs (?)
Eumonospora sp. of Cringoli et al., 1991 n. comb.

Japan (prefectures)
Tiba
Caryospora japonicum Matubayashi, 1936

Jordan
Caryospora maxima Modrý et al., 1999

Madagascar
Caryospora barnardae Upton, Freed, et al., 1990
Caryospora brygooi Upton, Freed, et al., 1990
Caryospora madagascariensis Upton, Freed, et al., 1990
Caryospora minuta Upton, Freed, et al., 1990
Caryospora serpentis Upton, Freed, et al., 1990

Malaysia (states)
Sabah
Caryospora kalimantanensis Modrý & Koudela, 1997

Mauritius (independent parliamentary republic of the UK)
Round Island (21 km NNE of Mauritius)
Caryospora durrelli Daszak et al., 2011a, b
Caryospora sp. of Daszak, 1995

Mexico
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020

Morocco
Eumonospora megafalconis (Klüh, 1994) Chou et al., 2020 (?)

Papua New Guinea (country in Oceania)
Caryospora sp. of Varghese and Yayabu, 1981

Peru
Caryospora epicrati Lainson et al., 1991, emended Modrý, 1998
Caryospora peruensis Upton et al., 1989

Portugal
Eumospora bubonis (Cawthorn & Stockdale, 1981) Chou et al., 2020
Eumonospora mochogalegoi (Cardozo et al., 2017) Chou et al., 2020
Eumonospora peneireiroi (Cardozo et al., 2016) Chou et al., 2020

Russia
Caryospora sp. 3 of Koudela et al., 2000
Caryospora sp. of Yakimoff & Matschulsky, 1936 (ovoidal form)
Caryospora sp. of Yakimoff & Matschulsky, 1936 (round form)
Eumonospora henryae (emend. Pellérdy, 1974) Chou et al., 2020

Saudi Arabia
Caryospora maxima Modrý et al., 1999
Caryospora saudiarabiensis (Modrý et al., 1999) Duszynski & Upton, 2010
Eumonospora biarmicusis (Alyousif et al., 2011) Chou et al., 2020
Eumonospora cherrughi (Alfaleh et al., 2013) Chou et al., 2020

Slovak Republic
Caryospora simplex Léger, 1911

Table 3. Alphabetical list of countries from which *Caryospora* and *Eumonospora* species have been described through 2023 (*continued*)

Thailand
Caryospora ahaetullae Modrý & Koudela, 1994
Caryospora sp. 2 of Modrý, 1998

Turkey
Caryospora sp. of Matuschka, 1986b

United Arab Emirates
Eumonospora boeri (Klüh, 1994) Chou et al., 2020
Eumonospora cherrughi (Alfaleh et al., 2013) Chou et al., 2020
Eumonospora falconis (Wetzel & Enigk, 1937) Chou et al., 2020
Eumonospora kutzeri (Böer, 1982) Chou et al., 2020
Eumonospora megafalconis (Klüh, 1994) Chou et al., 2020
Eumonospora neofalconis (Böer, 1982) Chou et al., 2020

USA (states)
Alabama
Caryospora spp. in dogs
Eumonospora tremula (Allen, 1933) Chou et al., 2020
Eumonospora uptoni (Lindsay & Blagburn, 1986) Chou et al., 2020
Arkansas
Caryospora duszynskii Upton et al., 1984a
Caryospora gracilis Upton, McAllister, et al., 1992
Caryospora lampropeltis Anderson et al., 1968
Caryospora masticophis Upton et al., 1994
Colorado
Caryospora duszynskii Upton et al., 1984a
Florida
Caryospora duszynskii Upton et al., 1984a
Caryospora relictae Telford, 1997
Caryospora tantillae Telford, 1997
Georgia
Caryospora bigenetica Wacha & Christiansen, 1982
Caryospora duszynskii Upton et al., 1984a
Caryospora ernsti Upton et al., 1984b (?)
Caryospora spp. in dogs
Illinois
Caryospora lampropeltis Anderson et al., 1968
Iowa
Caryospora bigenetica Wacha & Christiansen, 1982
Kansas
Eumonospora arcayae (Volcán & Medrano, 1984) Chou et al., 2020
Eumonospora hanebrinki (McAllister et al., 2013a) Chou et al., 2020
Eumonospora kansasensis (Upton, Campbell, et al., 1990) Chou et al., 2020
Eumonospora lindsayi (Upton, Campbell, et al., 1990) Chou et al., 2020
Eumonospora petersoni (McAllister et al., 2013b) Chou et al., 2020
Eumonospora tremula (Allen, 1933) Chou et al., 2020
Louisiana
Caryospora ernsti Upton et al., 1984b (?)
Caryospora natchitochesensis McAllister et al., 2014
Missouri (?)
Caryospora duszynskii Upton et al., 1984a
Caryospora spp. in dogs
New Mexico
Caryospora simplex Léger, 1911
Oklahoma
Caryospora choctawensis McAllister et al., 2013b
Caryospora duszynskii Upton et al., 1984a
Caryospora sargentae McAllister et al., 2022
Pennsylvania
Eumonospora microti (Saxe et al., 1960) Chou et al., 2020
Texas
Caryospora duszynskii Upton et al., 1984a
Caryospora gracilis Upton, McAllister, et al., 1992
Caryospora lampropeltis Anderson et al., 1968
Washington, D.C.
Eumonospora tremula (Allen, 1933) Chou et al., 2020

Venezuela
Eumonospora arcayae (Volcán & Medrano, 1984) Chou et al., 2020

Host location unknown/not given
Caryospora sp. of Frye, 1981
Caryospora sp. 1 of Koudela et al., 2000 (SE Asia)
Caryospora sp. of Upton & Sundermann, 1990

At least 2 other areas need additional attention and study, and, hopefully, the sooner the better. First, only 3 species, *C. bigenetica*, *C. duszynskii*, and *C. simplex*, have been studied *in vitro*, where their developmental stages were grown from SZs to oocysts or caryocysts. Even more importantly, only *E. daceloe, E. henryae, E. megafalconis,* and *E. neofalconis* have sequence data that has been generated and analyzed to aid in phylogenetic analysis of genetic relatedness. Both of these areas deserve intensive studies in the near future.

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